Biosystematics of the First-Stage Larvae of Some North American Bruchidae (Coleoptera)

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ABSTRACT

We studied first-stage bruchid larvae belonging to nine genera, three subfamilies, and the following 20 species: *Acanthoscelides aureolus, A. baboquivari, A. chiricahuae, A. collusus, A. macrophthalmus, A. mixtus, A. obtectus, A. prosopoides, Algarobius prosopis, Amblycerus acapulcensis, Caryobruchus gleditsiae, Mimosestes amicus, M. protractus, M. sallaei, Neltumius arizonensis, Sennius morosus, Stator limbatus, S. pruininus, S. pygidialis*, and *Zabrotes subfasciatus*. Representatives of each species were examined, and the prothoracic plate, spiracles, legs, and chaetotaxy were figured. Each species was described, and keyed; and their relationships, biology, and larval behavior were discussed.

The use of characters of larval insects in formulating classifications was discussed. We found that the initial larval forms to be described were those of economic significance or those that displayed unusual morphological characters. In some cases, larval characters provide a means of delineating adult taxa that were known to be different but could not be separated easily using adult characters.

The following characters were used: Presence, absence, lengths, number of segments, and complexity of development of the legs; type of tarsus; relative lengths, presence, absence, and distribution of setae; degree of development of prothoracic plate; presence or absence of median or anterior arms, or both, on the prothoracic plate; number of pairs of setae associated with the prothoracic plate; and larval behavior of wandering following eclosion, or penetrating the pod or seed directly upon hatching.

The larval and adult classifications were then compared. *Caryobruchus gleditsiae* was sufficiently unlike the other species to verify that it should remain as a member of a distinct subfamily (Pachymerinae). There is evidence based on larval morphology, that the genera *Zabrotes* and *Spermophagus* are only distantly related to the other genus in the subfamily Amblycerinae, *Amblycerus*. Classification of the subfamily Bruchinae shows some incongruence but not as much as the Amblycerinae.

Of those genera within the subfamily Bruchinae, adults and larvae of the genus *Mimosestes* show the greatest incongruency between classifications. According to the larval classification, *M. protractus* should be placed in a separate genus. There is some disagreement in the genus *Acanthoscelides*, since *A. macrophthalmus* and *A. chiricahuae* appeared to be more closely related to members of other genera. Consequently, they were placed in separate but neighboring polyphyletic assemblages. Aside from these discrepancies, considerable congruence exists among the adults and larvae of the remaining species, with the greatest congruence in the genus *Stator*.

The results of the Principal Component

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Analysis supported, to a large extent, an intuitive larval arrangement. The genus *Zabrotes* was placed closer to the genus *Stator* than to *Mimosestes protractus*, which differs from our phylogenetic groupings. *Acanthoscelides macrophthalmus* and *A. chiricahuae* appeared to be closely related and were grouped near the more advanced *Sennius morosus*. This arrangement coincided with the intuitive larval classification but differed from that of the adults. The remaining species showed little or no disagreement between either larval arrangement.

The function of the V-shaped neck fold and retractable head capsule, general body shape, tenth abdominal segment, anal aperture, and the long setae were discussed for the first time. The function of the V-shaped neck fold and retractable head capsule is to extend and increase the operational angle of the mouthparts during eclosion, pod or seed entry, and burrowing. The general body shape, when the broad thoracic and anterior abdominal segments are expanded by movement of haemolymph, aids in gaining purchase (leverage) necessary to overcome the backward thrust of the gnawing mouthparts. The tenth abdominal segment aids in locomotion by acting as a sucker disk, which becomes attached to the substrate, thus allowing the anterior end of the body to move freely about. Upon attachment to the substrate, it may also provide valuable purchase for the body when the larva is burrowing. The anal aperture, which

appears to be tripartite in species of the more primitive subfamilies, thus was likely associated with the primitive habit of wandering in search of a suitable host. It probably has been retained because of the apparent ease with which a Y-shaped lobe might be inverted when compared to an everted transverse lobe. Long setae appear to be largely tactile in function, whereas, the shorter, more stout setae appear more useful in gaining added purchase. The long, coiled setae between the appendages of most species appear to aid in disengagement of the distal end of the planted tarsi in preparation for forward movement. Long, coiled setae are wanting in those species in which appendages are absent.

Additional functions were determined for the (1) prothoracic plate (median arms); it appears that the teeth on the median arms become engaged first (before the teeth of the posterior arms), thus enabling the larva to gain purchase during the critical time of eclosion and pod or seed entry. (2) The spine on the first abdominal segment, in addition to stabilizing the body while the mandibles are working, appears to aid in rotation of the body within the egg and prior to eclosion. (3) Legs, in most cases, possess a flattened or rounded tarsus that terminates in an anteriorly directed lip. Within the egg or burrow, the lip is directed downward, thus providing additional resistance to the backward thrust of the body resulting from the activities of the mandibles.

INTRODUCTION

Most published works on larvae describe either economically important forms (Crouzel and others, *1968*)[2] or forms possessing what appear to be highly specialized traits (Clausen, *1940*; Maulik, *1931*). These and other works of their time are primarily concerned with the functional significance rather than taxonomic significance of the novel characters of larvae. It was not until the pioneering works of Böving (*1929*), followed shortly by Böving and Craighead (*1930*) and

others (Paterson, *1931*; Roberts, *1930*; van Emden, *1942*), that larval taxonomy finally began to receive attention. From the time of Linnaeus, phylogenies have been reconstructed on the basis of *a posteriori* evaluation of adult characters of insects; however, a noticeable trend is developing in which larval characters are receiving recognition in the interpretation of higher and lower taxa among insectan (Böving, *1929*; Evans, *1964*; Rozen, *1964*), as well as noninsectan groups (Orton, *1957*).

On the basis of larval characters, Roberts (*1939*) suggested that the beetle family

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[2]The year in italic, when it follows the author's name, refers to the Literature Cited, p. 43.

Erotylidae should not be split, as had previously been suggested, on the basis of adult characters. Commenting on Leng's "Catalogue of Coleoptera of America North of Mexico," Böving (*1929*) stated that genera, subfamilies, and even families would probably be rearranged after a thorough study of the larval forms. However, others at that time did not share his views. Crampton (*1930*), in comparing adult and larval morphologies of dipterans, suggested that larval characters were of little or no value because of the tremendous genetic and phenotypic plasticity possessed by the larval forms. Consequently, they express excessive "sideways developments" and exhibit too much mosaicism to be of value.

Although considerable congruency existed between larval and adult forms studied by Crampton, some of the larval forms were quite different and could not be classified as were the adults. He did state, however, that in developing a valid classification, characters of all stages should be considered—that is, larva, pupa, and adult—before reaching a final decision, but that where discrepancies exist, the adults should always be used in making a final decision, an opinion also shared by Maulik (*1931*). These comments were, of course, partially inconsistent with those expressed by Böving and Craighead (*1930*) in their discussion of the natural systematic grouping of the Coleoptera. They felt that a descriptive work was impossible without an understanding of the nature of characters throughout the order.

Rees (*1941*), in his work on the first instar of *Buprestis rusticorum* (KBY.), concluded on the basis of certain morphological characters that a new family should be recognized; whereas, Anderson (*1947*) argued that the genus *Cimberis* should be transferred to the family Anthribidae rather than remain in the family Curculionidae. Sanderson (*1948*) used larval host plants to provide evidence for speciation; whereas, MacSwain (*1956*) added behavior and ecology to delineate first instars of Meloidae.

Gordon (*1955*), followed shortly thereafter by the excellent review article of van Emden (*1957*), was the first to discuss thoroughly the significance of larval characters in the derivation of taxa. Van Emden discussed the theoretical and practical implications of subimaginal versus imaginal traits, and both authors concluded that larval characters tend to be of equal significance to those of the adults in the taxonomy of insects. Beal (*1970*) and Edmunds and Allen (*1966*) both concluded that adult and larval stages should have equal status.

Because little work has been done on larval Bruchidae and because there is considerable current activity on the classification of adult bruchids, we chose to work on this family of beetles. The Bruchidae are beetles whose adults, when they feed, feed primarily on the pollen and nectar of plants (Zacher, *1951*). According to Center and Johnson (*1974*), a broad range of host plants is attacked by the larvae of these seed beetles, primarily the family Leguminosae, but also some 30 other families.

A generalized life cycle of bruchids usually proceeds as follows: Adult bruchids lay eggs on the surface of pods or seeds. After a period of embryonic development, usually 5 to 10 days, the first instar emerges through the broad anterior end of the egg or directly through the venter of the egg into the seed or pod, using the egg chorion for leverage. If the larva exits through the anterior end of the egg, it may wander about seeking a suitable site for entry. After entering a seed, the larva feeds, molts several times, and eventually pupates, usually inside a single seed. The adult then emerges through a round exit hole.

A species of the Bruchidae may infest one plant species or the seeds of plants from several genera. In many species, only a single bruchid develops in each seed, however, in other species many larvae may be found in a single seed or a single larva may consume the cotyledons of several seeds (Center and Johnson, *1973*; Howe and Currie, *1964*; Johnson, *1967*; Riley, *1891*, *1892*).

Because some species of the Bruchidae compete directly with man for his beans, peas, and other valuable legumes, they are considered economic pests. Consequently, the work that has been completed on bruchid larvae has been concerned primarily with the biology and control of economically important species (Bondar, *1921*; Brindley, *1933*; Campbell, *1920*; Chittenden, *1898*; Howe and Currie, *1964*; Larson and Fisher, *1938*; Lepesme, *1942*; de Luca,

1956; Marcovitch, *1934*; Paddock, *1919*; Parnell, *1966*; Peake, *1952*; Pierce, *1930*; Randolph and Gillespie, *1958*; Riley, *1891*, *1892*; Slingerland, *1893*; Smith and Michelbacher, *1944*; Steffan, *1945*; Zacher, *1930*).

The morphology (Böving, *1927*; Eichelbaum, *1915*; Germar, *1818*; de Luca, *1968*; Parnell, *1964*; Patton, *1895*; Pfaffenberger, *1974*; Prevett, *1967*, *1968*, *1971*; Steffan, *1946*; Teran, *1962*, *1967*), and, in certain instances, functional morphology (Kunhikannan, *1923*; Lepesme, *1942*; Mukerji, *1939*; Zacher, *1930*), have been reported for a limited number of economic as well as noneconomic species.

Böving (*1927*) devised a species key to bruchid larvae but probably did not use first instars, judging from his measurements of the length of each species. He used characters relating to mouthparts, ocelli, and legs to derive his species classification.

Of the 1,300 described Bruchid species worldwide (Johnson, *1970*), only about 50 detailed larval descriptions are available. Of this total, 28 were described by Prevett (*1971*). Prevett derived his classification by using the following characters of the first instar: Spiracles, chaetotaxy, shape of setae, legs, and shape of tarsus, in conjunction with characters of later instars. He was, however, unable to distinguish between larvae at the species level.

Because the mouthparts of the first instar are, in most cases (for example, fig. 23, *Q* and *R*[3]), too minute to be accurately observed (Prevett, *1971*), we used characters relating to chaetotaxy, legs, tarsus, spiracles, anal aperture, behavior, and, in some instances, host plants to derive our system of classification.

The purpose of this study is to derive a system of classification of the first instars of the following species: *Acanthoscelides aureolus* (Horn), *A. baboquivari* Johnson, *A. chiricahuae* (Fall), *A. collusus* (Fall), *A. macrophthalmus* (Schaeffer), *A. mixtus* (Horn), *A. obtectus* (Say), *A. prosopoides* (Schaeffer), *Algarobius prosopis* (LeConte), *Amblycerus acapulcensis* Kingsolver, *Caryobruchus gleditsiae* (Linnaeus), *Mimosestes amicus* (Horn), *M. protractus* (Horn), *M. sallaei* (Sharp), *Neltumius arizonensis* (Schaeffer), *Sennius morosus* (Sharp), *Stator limbatus* (Horn), *S. pruininus* (Horn), *S. pygidialis* (Schaeffer), and *Zabrotes subfasciatus* (Boheman). Our larval classification is compared with the existing adult classification at the subfamily, generic, and species levels. We used traditional and numerical methods in our classification. Keys to the 20 species are provided, and the systematics and functional morphology of the larvae are discussed.

MATERIALS AND METHODS

Because of the difficulty encountered in associating larval bruchids with their adults, certain techniques were used to ensure the gathering of accurate data. To ensure accurate identification of each species, seeds or pods were taken from jars containing a single species of bruchid, and their eggs were removed and placed in screwcap vials, which were allowed to stand at room temperatures. Each vial was checked periodically with a dissecting microscope, and, upon eclosion, the larvae were removed and placed in vials containing 70 percent ethyl alcohol.

Some larvae were carefully dissected from the egg chorion. This procedure was employed only when the heavily pigmented head capsule and H-shaped prothoracic plate were visible,

because these were indications that the larva would probably hatch within minutes. Other specialized techniques were used to obtain first instars. Larvae of *Acanthoscelides prosopoides* were obtained by Forister and Johnson (*1971*) by allowing adult females to oviposit into open-celled styrofoam. We obtained them in the same way.

Information on larval behavior was obtained by observing the activities of live specimens or their damage to seeds and pods. Such activities of the bruchid larvae as where the larva had burrowed, the number of exuviae left within the burrows of the larvae,

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[3] All figures appear together, beginning on p. 47.

and the number of specimens within a seed were recorded.

Preparatory procedures similar to those of Prevett (*1971*) were used in obtaining microscopic slide preparations of entire larvae. A minimum of six specimens were observed for each species. Larvae were placed in a small crucible containing 60 percent lactic acid. The preparation was placed in an oven at 45° C for 8 to 12 hours. After the larvae had been cleared in lactic acid, they were positioned in a drop of Berlese's fluid. The mounting medium was placed on a 0.8–mm regulation size, depression slide. A coverslip was placed over the larva, compressing it in the position desired. After the coverslip had been positioned, it was sealed with clear fingernail polish.

A Wild M20 compound microscope, with a Zeichentubus camera lucida attachment, was used to illustrate all structures. The prothoracic plate was dissected from the larval integument and positioned so as to permit a complete dorsal view. The chaetotaxy and legs were figured while the larva was positioned laterally.

A system developed by Böving (*1927*) and adopted by Prevett (*1971*) was used to illustrate chaetotaxy. Rectangular diagrams (figs. 2 to 21) were drawn in which dotted lines were included to indicate sutures. These lines of demarcation divided the integument of the meso- and metathorax into prenotal and postnotal regions, dorsal epipleuron, ventral hypopleuron, and sternum. In addition, abdominal segments (figs. 24 to 43) 1 through 8 bear a spiracular region. The natural sutures were alined with the illustrated dotted lines and the setae were depicted.

Uppercase letters are used to designate primary (long) setae, whereas lowercase letters identify secondary (short) setae. The dorsum of the mesothoracic through abdominal segment 9 is divided by plicae. Consequently, the anterior, dorsal aspect of a segment is referred to as the prodorsum, and the letter D is used to label setae on that area of the integument. The setae appearing on the posterior, dorsal portion of a segment (postdorsum) are labeled with the uppercase or lowercase letters A and B.

Prevett (*1971*) used A, B, and C and their lowercase counterparts to denote the position of setae on the postdorsum. Because of the small size of first instars and difficulties associated with determining the exact location of each seta and because of variability within species, we used a different method. If there was only one primary seta per subsegment, it was designated as A, regardless of its position. The second and more ventral seta was designated as B. No "C" setae were found on species in this study. The use of lowercase letters paralleled that of the capitals. The lateral or pleural area is divided, by sutures, into a spiracular area (abdominal segments 1–8) and epipleuron. Identifying letters, for setae, appearing on these respective areas of the integument are s', or s'', or both; E, or e, or both; and H, or h, or both. The thoracic sterna of most larvae support a pair of elongate, coiled setae located between the thoracic appendages. These setae are labeled R. Thoracic legs of *Mimosestes protractus*, *Stator limbatus*, *S. pruininus*, and *Zabrotes subfasciatus* are lacking and have been replaced by pairs of setae. These setae are identified as K. *Acanthoscelides baboquivari* and *Amblycerus acapulcensis* possess an additional seta (f) near the base of the meso- and metathoracic appendages.

Abdominal sterna of most species have one to three short setae. These setae are identified with lowercase u, v, and x, depending on location, with the anterior seta labeled u; the middle, v; and the caudal, x. The dorsolateral seta on abdominal segment 10 is labeled g.

The prothoracic setae were identified by developing a composite illustration of all setae appearing on the prothoraces of the 20 species. The setae on the composite form are numbered consecutively (1 to 24), from dorsum to venter. The illustrations depicting the chaetotaxy on the prothorax of each species are then compared with the composite diagram. The numbers of those setae appearing on both illustrations are then recorded for each species.

Terminology similar to that of Prevett (*1971*) is used for describing the prothoracic plate and associated setal pattern (fig. 22, C). Each half of a prothoracic plate usually possesses anterior (A), median (M), and posterior (P) arms. Setae, in addition to being numbered consecutively, were distinguished by their relative locations between the anterior arms

of the prothoracic plate as either lateral, intermediate, or medial.

Legs were distinguished on the basis of degree of development and shape of the tarsus. Legs were either absent, two segmented with a flattened or rounded tarsus, or three segmented with an opposable (fig. 23, *J*) or immovable (fig. 23, *K*) claw.

The anal aperture was either Y-shaped or transverse.

Characters of the head were not used because Böving (*1927*) and Kunhikannan (*1923*) stated that head characters are not useful for separating larval forms of bruchids. Our observations agree with those of Prevett (*1971*), who observed the mouthparts of first instars to be too minute to illustrate.

Numerical analysis involved 22 arbitrarily selected variables (see p. 17), each of which could be assessed a value. These values were analyzed using the Principal Component Analysis (PCA) (Dixon, *1973*).

FUNCTIONAL MORPHOLOGY

Little has been done to ascertain the function of certain structures peculiar to the morphology of first instar Bruchidae. For this reason, we have included a discussion of functional morphology and how it may relate to larval behavior.

V-Shaped Neck Fold and Retractable Head Capsule

The V-shaped neck fold and retractable head capsule are typical of all known first instar Bruchidae (Kunhikannan, *1923*) and, inasmuch as these larval forms are all endophytic, their function is evident. Whether burrowing through the egg chorion, seed pod or test, or tunneling through seeds, the ability to retract and extend the gnawing mouthparts (head) is important. Prior to hatching, the larva positions itself forward in the egg, thus forcing the anterior end of the body against the dorsoanterior aspects of the egg chorion. This activity pushes the head back into the prothoracic and mesothoracic regions. The larva then moves its caudal segments forward, thus forcing haemolymph ahead, creating a general swelling in the anterior segments. Swelling may also be enhanced by swallowing air obtained through the chorion (Hinton, *1969*). Swelling in the anterior segments forces each lateral spine (located above the first abdominal spiracle) and the teeth of the prothoracic plate against the inner layer of the egg chorion, thereby stabilizing the position of the larva. The mouthparts (head) are then extended forward and begin eclosion. The larva gnaws through the soft, pliable, ventral surface of the egg (Mukerji, *1939*) in an anteroposterior direction. As the posterior portion of the emergence hole is being excavated, the head is extended posteroventrally, thus utilizing the V-shaped neck fold.

In those forms that bore directly from the egg into the pod coat or seed test, the larva relocates itself posteriorly in the egg chorion when the emergence hole is completed, thus forcing the caudal segments against the posterior aspects of the egg. By doing this, haemolymph is again forced into the anterior segments, creating the swelling necessary to gain needed leverage (see above). The retractable head capsule and the neck fold are then used when the larva begins gnawing into the seed or pod through the anteromedially located (Kunhikannan, *1923*; Mukerji, *1939*; Zacher, *1930*) emergence hole in the venter of the egg.

To a large extent, the above observations and interpretations support those of Howe and Currie (*1964*), Kunhikannan (*1923*), Lepesme (*1942*), and Zacher (*1930*) but differ from those of Mukerji (*1939*). According to Mukerji (*1939*), "The two anterior horns of the shield (anterior arms of the prothoracic plate) are clearly seen projecting anteriorly beyond the head capsule. These pointed ends pierced the tough wall of the egg-sac, and the rent so made was widened as the head was pressed forward permitting the larva to pass out from the egg-sac." Contrary to these observations, we have carefully removed eggs from the seed or pod surface, placed them ventral side up,

and observed larval hatching behavior. The larva definitely gnaws the emergence hole in the venter of the egg with its mandibles. Also, the hole is large enough to allow passage of the body by peristalsis, which, according to Lepesme (*1942*), occurs in a few seconds.

General Body Shape

According to Peake (*1952*), the general body shape, which consists of a broad head, thorax, and first through third abdominal segments, followed by a noticeable taper in the remaining abdominal segments (4-10), is typical of all known first instar bruchids except *Zabrotes subfasciatus* (Kunhikannan, *1923*). Its body is highly tapered toward the anterior as well as posterior ends. Some inherent advantages associated with this body shape were discussed in the previous section.

Briefly, the broadest portion of the body occurs in those areas where the greatest purchase (leverage) is gained for eclosion or burrowing into a seed or pod. As the posterior abdominal segments are brought forward, the movement of the body fluids into the anterior segments creates additional swelling, thus forcing the teeth of the prothoracic plate and the spines of the first abdominal segment against the wall of the burrow or inside of the chorion.

Some difficulty is encountered as the larva attempts to emerge through a rather small hole in the chorion. This problem may be overcome by peristaltic waves of muscular contraction that pass forward over the body surface (Wigglesworth, *1965*), thus squeezing the wider portions of the body through relatively narrow passageways. Nevertheless, many larvae do perish during eclosion because they are unable to escape through the emergence hole, especially those forms which do so through the anterior end of the egg. Apparently, once a larva has begun the process of eclosion, it cannot reenter the egg, possibly because of irreversible peristaltic waves or physical obstruction, or both, of the retrorse setae, spines, or prothoracic plate. Those forms that enter the seed or pod directly upon emergence probably experience lower mortality rates because of leverage gained from the seed or pod tissue by the use of the prothoracic plate.

Prothoracic Plate

The form of this structure varies considerably between species and has been used to delineate species by Kunhikannan (*1923*) and Böving (*1927*) and in this research. The function of the plate was studied by Kunhikannan (*1923*) in *Callosobruchus chinensis* and *Acanthoscelides obtectus*. Mukerji (*1939*) stated that Kunhikannan was in error based on evidence from Mukerji's studies. Our observations do not agree with those of Mukerji (*1939*) and Lepesme (*1942*), but do agree with those of Kunhikannan (*1923*) and Zacher (*1930*).

According to Lepesme (*1942*), the prothoracic plate has no known function and certainly does not serve to gain leverage as had been reported by Kunhikannan (*1923*). However, Lepesme thought that the posterior arms may serve to rasp away at the walls of the gallery, thus enlarging it for the remaining body segments. It is difficult to imagine that such a well-developed structure is not utilized in some manner for leverage during eclosion and pod or seed entry, or both.

Mukerji (*1939*) stated that the plate was essentially a "cephalic shield" used to protect the brain, which was not located in the chitinized head capsule. However, during eclosion he did say that as the larva assumes a curved posture, the teeth of the plate are firmly implanted into the flattened floor of the chorion. The head is then thrust forward, and the mandibles gnaw a small hole in the floor of the egg. We believe that his explanation would necessitate an extensible fold of integument between the base of head capsule and the anterior aspects of the first abdominal sternite (which has not been observed to date) to enable the mouthparts to reach the floor of the egg. In addition, he made no mention as to the use of the plate during seed entry.

According to Kunhikannan (*1923*), the plate is used to gain purchase both during eclosion and pod or seed entry, or both. Afterwards, the plate is lost during the first molt, and the larva moves persistaltically within the burrow.

According to Zacher (*1930*), "The function of the neckplate in *Zabrotes* is entirely obvious, it provides support for the larva near the end of the egg stage. It requires this support to completely eat through the egg shell and the seed

coat, as well as through the hard cement between the egg and seed coat."

Although the function of the plate has been discussed, the significance of the median arms has yet to be defined. As observed from lateral (Prevett, *1967, fig. 1A*) and anterodorsal (Kunhikannan, *1923*) views, the teeth of the median arms are located anteromedially to the teeth associated with the posterior arms. Their strategic location enables the larva to obtain purchase on the seed test or pod pericarp, while the teeth of the posterior arms are free or are still within the chorion of the egg, thus enabling the larva to apply force to the mandibles. The teeth of the median arms may be in close proximity because it is much easier to get these teeth through the emergence hole than it would be to try to wedge the teeth of the posterior arms through. It would also seem that the functional significance of these teeth would be largely negated once the larva has tunneled into the seed, for at this time the plate would be largely depressed into the thorax, thus creating considerable resistance to forward movement.

Spine on First Abdominal Segment

The function of this structure was overlooked by Kunhikannan (*1923*) but has since been discussed both as an egg burster (Howe and Currie, *1964*; Mukerji, *1939*; Teran, *1962*; van Emden, *1946*) and a fulcrum used by the larva to emerge from the egg (Howe and Currie, *1964*; Teran, *1962*; Zacher, *1930*).

In addition to functioning with the V-shaped neck fold and retractable head capsule during eclosion, this spine appears to have another function (Howe and Currie, *1964*; Zacher, *1930*). From our observations of emerging specimens, it appears as though the spines are manipulated with ease; that is, their distal ends (Mukerji, *1939*) may be extended at right angles to the body or returned to a position paralleling the integument. Muscles are probably inserted at the base of the spine.

Another function is one of assistance in rotation within the egg prior to emergence (Howe and Currie, *1964*). Recorded observations on embryonic development of bruchid larvae indicated that most develop with their

venter opposite the surface of the pod or seed. Therefore, rotation must occur within the egg before eclosion can occur. Rotation is executed with the combined efforts of the abdominal spines, prothoracic plate, and, to a lesser extent, the body setae. By peristaltic contractions, a slight torsion of the body, and alternating usages of the spines and prothoracic plate, intervened by the stabilizing effect of the body setae, the larva is able to right itself within the egg preparatory to emergence.

Legs

The lengths of the legs may vary from those in which each pair is exceeded in length by the next posterior pair or those in which all are of subequal lengths to those in which legs are completely wanting. Kunhikannan (*1923*) described the functional significance and activity of those legs of varying lengths in his behavioral discussion of *Acanthoscelides obtectus*. We have observed these larvae penetrating the free surface of a pod or seed. Thus, his description of the process in which the larva loops the body and uses the legs to create additional pressure on the mandibles, by shifting the weight and forces of the body forward, appears acceptable at this time contrary to opinions expressed by Mukerji (*1939*).

The habit of boring directly into the seed or pod from the egg would seem to negate the value of legs, unless they were used for burrowing by the larva. If they are used for burrowing, we feel that their lateral arrangement would be an advantage. An explanation for this may be that of the species involved in this study that possess legs, only *Amblycerus acapulcensis* and *Caryobruchus gleditsiae* (figs. 23, *J* and *K*) lack a tarsus that terminates in a flattened or rounded anteriorly projecting lip. In the egg or burrow where the legs are arranged posteroventrally, the lip of the tarsus would be directed outward. As the larva begins to burrow, it would move its posterior segments forward, thus forcing the haemolymph into the anterior segments. As a result, the anterior segments would swell, forcing the lip of the tarsus into the tissue of the cotyledon. This would provide additional stabilization for the larva in overcoming the

backward thrust of the body resulting from the activities of the mandibles.

Conversely, we believe the lip of the tarsus would also present a problem in moving forward through the burrow because of drag and the chances of snagging on the walls of the burrow. This may be one reason why larvae molt soon after entering the seed.

The legs of *Amblycerus acapulcensis* are probably adapted primarily for walking since this bruchid appears to have little difficulty in burrowing through the pod wall without gaining purchase. The legs of *Caryobruchus gleditsiae* are very stout and terminate in a very sharp, heavy claw. Because its host seed is extremely hard, the legs (claws) are probably actively used while boring into the seeds. Apodous forms may lack appendages because the legs may have presented more of an obstacle than assistance. This probably accounts for the apodous larva of *Mimosestes protractus*. It enters the very green pods of *Prosopis juliflora*, and the legs probably would provide little assistance and considerable drag in trying to move through the sirupy contents of the pod. Consequently, the appendages were probably selected against.

Tenth Abdominal Segment

All the species in this study appear to use the tenth abdominal segment as an adhesive disk, thus serving a very important function in locomotion (Kunhikannan, *1923*; Peake, *1952*). Larvae of *Amblycerus acapulcensis* were observed to crawl a short distance, then loop the body, bringing the caudal end forward. The tenth segment sucker then became attached to the substrate, and the larva rose to a vertical position. There it swayed back and forth several times before it resumed its horizontal position.

On many occasions, the larva of *A. acapulcensis* also moved forward in short incre-

ments, much like an inchworm (Geometridae) (Peake, *1952*). This mode of behavior sometimes occurred for several seconds before the larva resumed walking.

Setae

The long setae of the larvae of ancestral bruchids doubtlessly possessed a tactile or protective function as the larva crawled over the pod or seed surface. However, because many of the first instar larvae no longer exhibit this form of behavior, we suspect that the primary setae have regressed in length because the setae show a definite trend in change of length from the long (more active larvae, thus probably more primitive) primary setae to the complete absence of primary setae (typical of more sedentary larvae, thus probably more derived).

In most instances, the prothoracic primary setae do not equal the lengths attained by the primary setae located on other body segments. Apparently, the short setae are more easily manipulated through the emergence hole. Once this happens, the larva has gained additional leverage, which is so essential in successfully escaping from the egg.

Setae that appear on the thoracic sternites of many forms are large and coiled (fig. 8). According to Kunhikannan (*1923*), they "secure sufficient space between the ventral surface and the seed for the meal to be worked back, for an intimate contact with the seed on the ventral side would make difficult the passage of the meal." They might also function indirectly in burrowing. As the burrow is lengthened, the head is extended forward, thus reducing the pressure of the body fluids in the thoracic segments. In conjunction with the reduced pressure and what appears to be a springlike seta, the thoracic sternites would probably be elevated, thus allowing the larva to disengage the lip of its tarsus in preparation for the forward movement of the body.

SYSTEMATICS OF SOME FIRST INSTAR LARVAE OF THE BRUCHIDAE

Morphological Characters

External morphology, behavior, and (to a

limited extent) host plants were used to derive the following larval group arrangements and stepwise component analysis (fig. 44):

LARVAL GROUPS AND SUBGROUPS

1. *Amblycerus acapulcensis*
2. *Caryobruchus gleditsiae*
3. A. *Algarobius prosopis*
   B. *Acanthoscelides obtectus*
   C. *A. prosopoides*
   D. *A. collusus*
      A. mixtus
      A. aureolus
   E. *A. baboquivari*
4. A. *Mimosestes sallaei*
   B. *M. amicus*
   C. *Acanthoscelides macrophthalmus*
5. A. *A. chiricahuae*
   B. *Neltumius arizonensis*
   C. *Sennius morosus*
6. *Stator pygidialis*
   S. pruininus
   S. limbatus
7. *Mimosestes protractus*
8. *Zabrotes subfasciatus*

Characters that proved to be of greatest value were those associated with—

● Prothoracic plate: Number of teeth present on median and posterior arms; presence or absence of median arms; number of associated setal pairs; gross morphology; shape of some teeth; degree of development.
● Legs: Presence, absence; number of segments; degree of development of tarsus; shape of tarsus; relative lengths of legs; associated setal arrangements and sensory pores.
● Anal aperture: Shape.
● Spiracles: Uniforous, biforous, and location.
● Setae: Distribution on different intrasegmental areas; presence or absence of primary setae; varying lengths of primary setae; reduction in setal number.

Nonmorphological Characters

When known, host specificity and larval behavior were used in our classification. We used such attributes of larval behavior as whether the larva bores directly into a seed or pod, or ecloses through the anterior end of an egg and uses the chorion to gain leverage, or ecloses then wanders before entering a seed.

Species Groups

The larvae of the 20 species we studied display a definite trend in reduction of develop-ment or loss of structures from what we consider to be more ancestral (*Caryobruchus gleditsiae* and *Amblycerus acapulcensis*) to the more derived forms (*Zabrotes subfasciatus* and *Mimosestes protractus*). We consider ancestral structures to be those composed of numerous parts and less reduced in size, whereas derived structures exhibit a loss of, or reduction in size of, component parts (Brown, *1965*).

The characters we considered to be derived were—

● Setae: Reduction in relative lengths of both primary and secondary setae and a reduction in number.
● Prothoracic plate: Reduction in degree of development, numbers of teeth on median and posterior arms, and setal pair number associated with plate; loss of median arms and majority of posterior arms.
● Legs: Reduction in number of segments and development of tarsus.
● Spiracles: From biforous to uniforous.
● Anal aperture: From Y-shaped to transverse.
● Larval behavior: After hatching, larvae that crawl over the pod or seed surface prior to entering the host are considered to be most ancestral (in the sense of MacSwain, *1956*); whereas, those that penetrate the pod or seed directly upon eclosion we regard as being more derived.

Group 1.—This group, composed of only *Amblycerus acapulcensis*, is considered to be most primitive because it has (1) three-segmented legs possessing internal sclerotized plates (fig. 23, *J*) and terminates in a movable, opposable claw; (2) biforous spiracles; (3) a Y-shaped anal aperture; and (4) a well-developed prothoracic plate with median arms and five pairs of associated setae (fig. 22, *J*). This group is thought to be more closely related to group 2 than to other groups because both possess biforous spiracles, Y-shaped anal apertures, three-segmented appendages, and more than four pairs of setae associated with the plate. Group 1 is separated from group 2 because group 1 possesses median arms on the prothoracic plate and one pair of primary and two pairs of secondary setae on the dorsum of the 10th abdominal segment (fig. 33).

Group 2.—This group, composed of *Caryobruchus gleditsiae*, is distinguished by the absence of (1) median arms on the prothoracic plate (fig. 22, *K*), (2) opposable claws on the legs, and (3) primary setae on the 10th abdominal segment. The reduction in length of abdominal primary setae indicates that group 2 is probably more derived than group 1. The presence of four pairs of setae on the postdorsum of abdominal segments 2–7 (fig. 34) and a primary and secondary hypopleural seta on abdominal segments 5 and 8 easily separate groups 1 and 2. Because groups 2 and 3 are distantly related, many noticeable morphological differences exist between them. Biforous spiracles, a Y-shaped anal sulcus, and seven pairs of setae associated with the prothoracic plate represent a few of many possible characters that may be used to separate the two groups.

Group 3.—The seven species of this group are recognized by the presence of 8 to 10 pairs of setae on the prothorax (fig. 2), exclusive of those associated with the prothoracic plate. These species are also similar in gross morphology of the prothoracic plate (fig. 22), number and distribution of setae associated with the plate, and each pair of legs being exceeded in length by the succeeding pair (except *Acanthoscelides baboquivari*). We separate subgroups 3*A*, *B*, and *C* from subgroups 3*D* and *E* on the basis of larval behavior. The first instar of groups 3*A*, *B*, and *C* crawls over the pod or seed surface following eclosion, whereas the first instar of groups 3*D* and *E* bores directly from the egg into the pod or seed.

Subgroup 3A.—This subgroup, composed of *Algarobius prosopis*, differs in that it has a single tooth on each median arm and seven teeth on each posterior arm of the prothoracic plate (fig. 22, *I*), and the mesothoracic spiracle is located on the epipleuron instead of the hypopleuron as in the other groups. We consider this subgroup to be related to subgroup 3*B* since both subgroups exhibit similarities in their prothoracic plates (fig. 22, *G* and *I*), chaetotaxy (figs. 8, 10, 30, and 32), and larval behavior.

Subgroup 3B.—*Acanthoscelides obtectus* differs from others in group 3 in possessing a single tooth on the median arms and five teeth on each posterior arm of the prothoracic plate (fig. 22, *G*). It also possesses broad sclerotized plates on the dorsum of abdominal segments 8 and 9 (fig. 30). The number of teeth on the median arms (fig. 22, *G* and *H*) and the absence of primary setae on the postdorsum of abdominal segments 1–7 (figs. 30 and 31) are differences between subgroups 3*B* and *C*.

Subgroup 3C.—*Acanthoscelides prosopoides* is more nearly related to subgroup 3*B* than to subgroup 3*D* because of differences in larval behavior and host plant preferences. It differs from subgroup 3*B* by lacking abdominal plates (fig. 30) and long, curved setae at the distal end of the basal leg segment (fig. 23, *G*), and by possessing two secondary setae on the postdorsum of abdominal segments 1–7 (fig. 31). *A. prosopoides* and *A. collusus* are alike because both possess two teeth on each median arm of the prothoracic plate.

Subgroup 3D.—*Acanthoscelides collusus, A. mixtus*, and *A. aureolus* are very closely related. *A. aureolus* and *A. mixtus* are thought to be more closely related because of nearly identical prothoracic plates (fig. 22, *A* and *F*), presence of seta *d'* on the prodorsum of the mesothoracic and metathoracic segments (figs. 2 and 7), and larval behavior. These two species are, however, readily separated by three postdorsal and one epipleural setae on abdominal segment 9 of *A. aureolus* (figs. 24 and 29), which *mixtus* lacks. The larva of *A. collusus* may wander after eclosion, which resembles the behavior of those larval forms in subgroups 3*A*, *B*, and *C*. *A. collusus* also possesses two teeth on each median arm of the prothoracic plate (fig. 22, *D* and *H*), which is similar to *A. prosopoides* and differs from *A. aureolus* (fig. 22, *A*) and *A. mixtus* (fig. 22, *F*). *A. collusus* also possesses primary and secondary setae on the mesothoracic epipleuron (fig. 5) as do *A. aureolus* (fig. 2) and *A. mixtus* (fig. 7) but is wanting in *A. prosopoides* (fig. 9). In addition, *A. collusus* enters the pod or seed directly from the egg, which *A. prosopoides* has not been observed to do, thus more closely approximating behavioral characteristics of *A. aureolus* and *A. mixtus*.

Subgroup 3E.—*Acanthoscelides baboquivari* is easily separated from the other subgroups because of its greatly reduced pair of prothoracic legs (fig. 23, *B*) and presence of

seta f on the meso- and metathoracic sterna (fig. 3).

Group 4.—Mimosestes sallaei, M. amicus, and *Acanthoscelides macrophthalmus* resemble one another more closely than they do any other species group. Because of this, they are placed together in this group. The prothoracic plate of each species, which serves to distinguish group 4 from other groups, has two teeth on each median arm and an elongate, pointed, median tooth subtended by seven or eight smaller, blunt teeth on the posterior arms (fig. 22, *E, L,* and *N*). The chaetotaxy is also similar on the epi- and hypopleural regions of the mesothorax and metathorax (figs. 6, 13, and 15) and most abdominal segments (except segments 1, 2, and 5) (figs. 28, 35, and 37).

Subgroup 4A.—Mimosestes sallaei is readily distinguished because each pair of legs is longer than the preceding pair, and each leg terminates in a flattened tarsus (fig. 23, *M*). *M. sallaei* also possesses seta *s'* above the first abdominal spiracle (fig. 27).

Subgroup 4B.—Mimosestes amicus is separated from subgroup 4A by its thoracic appendages of subequal lengths (fig. 23, *L*). The flattened tarsus and larval behavior serve to distinguish it from subgroup 4C.

Subgroup 4C.—Acanthoscelides macrophthalmus differs from these similar forms because its legs are of subequal lengths and each terminates in a rounded tarsus (fig. 23, *E*). The prodorsal region of the meso- and metathorax (fig. 6) possesses three setae. A pair of setae are also present at the base of each appendage.

*Group 5.—*As in group 4, *Acanthoscelides chiricahuae, Neltumius arizonensis,* and *Sennius morosus* probably represent a polyphyletic assemblage. Each species has legs that terminate in a rounded tarsus (fig. 23, *C, N,* and *O*). This character separates this group from the others, with the possible exception of subgroup 4C. However, the metathoracic appendage of *A. macrophthalmus* terminates in a tarsus, which is more flat than rounded.

Subgroup 5A.—Acanthoscelides chiricahuae is thought to be related more to *Neltumius arizonensis* than to *Sennius morosus* because of the complete absence of sternal setae on the abdomen of *S. morosus* (fig. 39). This subgroup

is most easily recognized by the hypopleural setae on the mesothorax and metathorax (fig. 4) and abdominal segment 9 (fig. 26). It also possesses three teeth on one median arm and two teeth on the other median arm of the prothoracic plate (fig. 22, *C*).

Subgroup 5B.—Neltumius arizonensis is distinguished by the presence of three to four teeth on the median arms and five to six on the posterior arms of the prothoracic plate (fig. 22, *O*). It also infests the seeds of *Prosopis* and has comparatively shorter setae than those of subgroup 5A (figs. 16 and 38).

Subgroup 5C.—Sennius morosus is easily separated by the absence of setae on the abdominal sternites (fig. 39) and presence of two teeth on each median arm of the prothoracic plate (fig. 22, *P*).

*Group 6.—*The larvae of *Stator pygidialis, S. pruininus,* and *S. limbatus* lack legs and primary setae (figs. 18, 19, 20, 40, 41, and 42). This distinguishes them from groups 1 through 5. Group 6 differs from groups 7 and 8 because larvae in group 6 have an elongate, pointed median tooth on the posterior arms of the prothoracic plate (fig. 22, *Q, R,* and *S*).

Stator pygidialis and *S. pruininus* are thought to be very closely related because both share numerous similarities in chaetotaxy and morphology (figs. 19, 20, 41, and 42). They also possess nearly identical prothoracic plates (fig. 22, *R,* and *S*), usually differing only in a single tooth on the median arm of the prothoracic plate of *S. pruininus*. In addition to this difference, *S. pygidialis* possesses eversible saclike lobes on the thoracic sterna (fig. 20) and lacks the several pointed, sclerotized, plates on abdominal sternites 7 and 8 of *S. pruininus* (fig. 41).

S. limbatus is easily separated because it has five teeth on each posterior arm of its prothoracic plate as compared with three teeth in *S. pruininus* and *S. pygidialis*.

Group 7.—Mimosestes protractus is easily separated from members of groups 1 through 5 by the absence of primary setae and legs. The absence of the elongate, median tooth on the posterior arm of the prothoracic plate and the four pairs of associated setae (fig. 22, *Q, R,* and *S*) serve to distinguish this group from group 6. Characters of the prothoracic plate also sepa-

rate group 7 from group 8. Each arm of the prothoracic plate of group 8 (fig. 22, *T*) is represented by two or three teeth (thought to be remnants of the posterior arms), whereas the prothoracic plate of group 7 (fig. 22, *M*) possesses anterior, median, and posterior arms.

Group 8.—This group, composed of *Zabrotes*

subfasciatus, is separated from all other groups by the absence of primary setae, legs, (figs. 21 and 43), and a nearly complete reduction in the prothoracic plate (fig. 22, *T*).

Morphological differences between species of groups 7 and 8 are so distinct they do not need further discussion.

CLASSIFICATION OF LARVAL BRUCHIDAE AT THE SUBFAMILY AND GENERIC LEVELS

Böving (*1927*) and Prevett (*1971*) classified bruchid larvae at the subfamily level but primarily used characters of the intermediate instars. Prevett was the first to use characters of the first instar in a subfamily classification.

We compared characters of the first instars of species in this study to see if we could arrive at a subfamily classification that would conform to the adult subfamily classification. We compared the chaetotaxy, prothoracic plates, legs, and anal segments. These characters were then compared with characters Prevett used in his classification. Except for chaetotaxy, our results were generally inconclusive, indicating that additional characters and species need to be studied or that there is incongruence between larval and adult classifications at the subfamily level.

Chaetotaxy

Our observations and those of Prevett (*1971*) indicate that the chaetotaxy of the first instars may be useful to separate subfamilies. The setae of the spiracular area of abdominal segments 2–8, the hypopleura of abdominal segments 2–9, abdominal sternites 2–8, and the prodorsum of the meso- and metathorax all are valuable to distinguish the Pachymerinae, Amblycerinae, and Bruchinae. In the Pachymerinae, *Caryobruchus*, *Caryedon*, and *Pachymerus* all have secondary setae in the spiracular area of abdominal segments 2–8. Their abdominal hypopleura (2–9) are variable because some segments bear a single seta, whereas others have two. The chaetotaxy of abdominal sternites 2–8 also appears variable, but there are usually more than two setae or less than two setae on each

sternum. *Caryobruchus* and *Caryedon* are without setae on the prodorsum of the meso- and metathorax, whereas seta *d'* is present in *Pachymerus cardo*.

Setae are not as common on the spiracular areas of abdominal segments 2–8 in the Amblycerinae as they are in the Pachymerinae. *Amblycerus acapulcensis* possesses one seta, on the spiracular area of abdominal segments 7 and 8, that separates it from the Pachymerinae. *Zabrotes subfasciatus* is without setae, whereas *Spermophagus* sp. bears one seta in the spiracular area. Members of Amblycerinae are consistent in that only a single secondary seta appears on the hypopleuron of abdominal segments 2–9. The condition that exists in the chaetotaxy of the spiracular and hypopleural areas of *Z. subfasciatus* is also typical of many Bruchinae. However, *Z. subfasciatus* may be distinguished from species of Bruchinae by the presence of a single secondary seta on the meso- and metathoracic epipleuron. The Amblycerinae consistently bear setae *u* and *v* on abdominal sternites 2–8. This subfamily is also the only subfamily that consistently lacks setae on the meso- and metathoracic prodorsa.

Except for *Mimosestes protractus*, which has one seta on the spiracular area of the second abdominal segment, the Bruchinae lack setae on all abdominal spiracular areas. However, in this subfamily the arrangement of the setae does not follow a consistent pattern on the abdominal hypopleura and sternites. A majority of the Bruchinae also lack setae on the prodorsum of the meso- and metathorax, but others may possess two or three setae.

In summary, the Pachymerinae are most easily distinguished from the other sub-

families by two setae on the spiracular areas of abdominal segments 7–8. The Amblycerinae may be distinguished by a combination of the single seta (*h*) on abdominal hypopleura 2–9 and the presence of not more than one seta on the spiracular area of abdominal segments 7 and 8. *Zabrotes subfasciatus* (Amblycerinae) first instars resemble many species in the Bruchinae in many characters, including the lack of spiracular setae. *Z. subfasciatus* may be separated from the Bruchinae, however, by the single secondary seta on its meso- and metathoracic epipleura. The Bruchinae are distinguished from the other subfamilies because they lack spiracular setae. *M. protractus* (Bruchinae) possesses one spiracular seta on the second abdominal segment but also possesses two secondary setae on the prodorsum of the meso- and metathorax, which is sufficient to distinguish it from the Amblycerinae and Pachymerinae.

Prothoracic Plate

Caryobruchus gleditsiae is easily distinguished from other species in this study by the absence of median arms and the presence of seven pairs of associated setae. Prevett (*1971*) cited the absence of setae on the sclerotized plate as a consistent difference between the Pachymerinae and the other two subfamilies he treated. We found that this is not true of *C. gleditsiae* (fig. 22, *K*). Conversely, characters we used to distinguish the Pachymerinae are not of value in separating members of the same subfamily in Prevett's study, because members of *Caryedon* appear to possess median arms and fewer numbers of setae (four pairs). We were unable to find characters, of the prothoracic plate, that link together members of the Pachymerine genera *Caryedon*, *Pachymerus*, and *Caryobruchus*.

The two species we studied in the Amblycerinae have prothoracic plates that are extremely different from one another. The plates of *Amblycerus acapulcensis* (fig. 22, *J*) and *Zabrotes subfasciatus* (fig. 22, *T*) seem to represent extremes in degrees of development, whereas that of *Spermophagus* sp. (see fig. 22 *A* in Prevett, *1971*) is reduced in development and appears to have a form intermediate to that of the other two species. Today

no characters of the prothoracic plate appear to link together members of the Amblycerinae.

As stated by Prevett, with the exception of *Bruchidius schoutedeni* (Pic) (Prevett, *1971*: fig. 23, *G*), the plates of the Bruchinae appear X-shaped and may be used to distinguish this subfamily. The plate of *B. schoutedeni* may be distinguished by its V-shape and the presence of three pairs of setae on the sclerotized plate. Some members of the genus *Caryedon* (Prevett, *1971*: fig. 15) also possess an X-shaped plate. We found that seta 5 (fig. 22, *C*) appears to be a consistent character to most Bruchinae, but apparently not to *Caryedon*. Seta 5, then, separates these two groups.

Legs

The legs of *Caryobruchus gleditsiae* are quite well developed, possessing a distinct coxa, femur, and tibia which terminates in a very heavy claw. Prevett stated that the appendages of the Pachymerinae he studied were composed of four segments; however, we could only find three segments in the legs of *C. gleditsiae*. Consequently, the number of segments in their legs apparently does not link members of this subfamily.

The legs of *Amblycerus acapulcensis* are the most highly developed of those species involved in this study. They have four segments with the three distal segments possessing internal sclerotized plates (fig. 23, *J*). There is a great deal of similarity between the appendages of *A. acapulcensis* and *Pachymerus cardo* (Prevett, *1971*: fig. 11a).

Böving (*1927*) observed that *Spermophagus hoffmanseggi* Gyllenhal had "three pairs of rather long legs . . ." A leg of this species was subsequently illustrated by Böving and Craighead (*1930*). Kingsolver (*1970*) transferred the adults of this species to the genus *Amblycerus* where they rightfully belong. Prevett (*1971*) remarked that this species was not similar to others in the Amblycerinae. Böving's studies of *Amblycerus hoffmanseggi* support ours: Species in the genus *Amblycerus* have elongate legs. Species of the true genus *Spermophagus* and of *Zabrotes* appear to be apodous.

According to Prevett, appendages of the Bruchinae are three segmented. The third

segment, one more than had previously been found (Kunhikannan, *1923*; Riley, *1891*), Prevett termed a "poorly defined" coxa. This basal segment may occur in all Bruchinae, but it is so small and difficult to see that we cannot verify that all the Bruchinae that we studied have three-segmented legs. The legs of some Bruchinae are flattened terminally, whereas others are rounded (fig. 23, *A,D*, compare with *C*). The Bruchinae *Stator limbatus*, *S. pruininus*, *S. pygidialis*, and *Mimosestes protractus* lack appendages as does *Eubaptus rufithorax* (see fig. 42 in Teran, *1967*), several species of the subfamily Amblycerinae, and species of *Tuberculobruchus* (Prevett, *1971*).

Due to the presence, degree of development, or absence of legs among the members within the three subfamilies, it does not appear possible at this time to distinguish one subfamily from another on the basis of leg development.

Spiracles

Members of the Bruchinae may be distinguished by their uniforous spiracles, whereas the spiracles of the Pachymerinae are biforous. The biforous spiracular condition constitutes a subfamilial character, which may be used to distinguish the Pachymerinae. In the Amblycerinae, the genera *Zabrotes* and *Spermophagus* have spiracles that are uniforous, but *Amblycerus* has biforous spiracles.

Anal Segment

A comparison of the first instar anal segment was not made by Prevett (*1971*) nor had one been made previously; therefore, the following statements refer only to species in this study. A consistent feature of all Bruchinae and *Zabrotes subfasciatus* is the two-lobed anal segment created by a transverse anal aperture, but *Caryobruchus gleditsiae* and *Amblycerus acapulcensis* are characterized by a Y-shaped anal sulcus, which divides the tenth segment into three lobes.

We used many characters in an attempt to arrive at a classification at the generic level that matched that of the adults. This we were unable to do. More characters and species need to be studied before a generic classification of first instar New World bruchid larvae is formulated.

CONGRUENCE BETWEEN A LARVAL AND AN ADULT CLASSIFICATION OF BRUCHIDAE

When the larval classification at the species level had been completed, it was compared with a species classification of the adults. This was something of a problem because, although there has been a good deal of research on the Bruchidae in recent years, little work has been done on the relationships between taxa at the generic level and above. Therefore, the adult classification below was compiled from a key by Bridwell (*1946*), Slobodchikoff and Johnson (*1973*), personal communications with J. M. Kingsolver, and unpublished data of one of us (Johnson). The following classification of the adults is presented so that those species that are listed close to one another we believe are most closely related:

CLASSIFICATION OF SOME ADULT BRUCHIDAE

Subfamily Pachymerinae
  Caryobruchus gleditsiae
Subfamily Amblycerinae
  Amblycerus acapulcensis
  Zabrotes subfasciatus
Subfamily Bruchinae
  Mimosestes amicus
  M. sallaei
  M. protractus
  Algarobius prosopis
  Acanthoscelides macrophthalmus
  A. chiricahuae
  A. obtectus
  A. prosopoides
  A. aureolus
  A. collusus

CLASSIFICATION OF SOME ADULT
BRUCHIDAE—Continued

Subfamily Bruchinae—Continued

    A. mixtus
    A. baboquivari
    Sennius morosus
    Stator limbatus
    S. pruininus
    S. pygidialis

The subfamilies Amblycerinae, Pachymerinae, and Bruchinae are quite distinct from each other, at least in the adult stages, and are believed to represent natural groups. Recent studies, however, indicate that *Zabrotes* and *Amblycerus*, genera of the Amblycerinae, may not be as closely related to one another as was once thought (J. M. Kingsolver, personal commun.).

When characters of the adults are used, species in the genera *Mimosestes*, *Algarobius*, and *Acanthoscelides* form an apparent, natural, cohesive group. Species of *Sennius* and *Stator* have many characters in common and appear to be more closely related in the characters of the adults than to others treated here. The genus *Neltumius* lacks close affinities to other groups known to us.

The classification of species larval characters for the most part matches that of the adults (fig. 44). *Amblycerus acapulcensis* and *Caryobruchus gleditsiae* are both distinct and, based on larval characters, should probably be placed in separate subfamilies. Species in the other genera generally are clumped together in a classification much like that of the adults. Minor exceptions are that *Acanthoscelides macrophthalmus* (group 4) is more similar to *Mimosestes amicus* and *M. sallaei*, and group 5 is composed of three species from three different genera. It was pointed out previously that groups 4 and 5 (p. 12) are probably artificial, so these exceptions are probably not of any great significance.

Congruence between adult and larval classifications is probably best exemplified by the three species in the genus *Stator*. The species show close relationships whether adult or larval characters are used.

Incongruence is most striking between the adult and larval classifications of both *Mimosestes protractus* and *Zabrotes subfasciatus*. Larvae of both species resemble larvae in species of *Stator*. The differences from other larvae are especially apparent in the Principal Component Analysis (PCA) (fig. 44). The adults of *M. protractus* are quite distinct from other known species of *Mimosestes*, therefore radical differences are not so surprising. It is with *Z. subfasciatus* that the incongruence between the adult and larval classification is most noteworthy. *Zabrotes* and *Amblycerus* adults are classified in the same subfamily, yet the larvae are very different. In the list on page 10, they are classified at opposite ends of a "phylogenetic" series of larval groups, and they also appear distant from one another in figure 44.

Minor incongruence is shown in both *Sennius morosus* and *Neltumius arizonensis*. Adult characters do not closely ally *N. arizonensis* with any known bruchids (except other *Neltumius*), but larval characters loosely ally it to both *Acanthoscelides chiricahuae* and *S. morosus*.

It comes as no surprise that there is some incongruence between larval and adult classifications of bruchids. First instars of the Bruchidae are highly modified for entry into seeds, whereas the imagos are specialized for reproduction.

As far as is known, adults most often feed on pollen and nectar in flowers. It seems to us that the very great difference in habitat and the resultant differences in selection pressures would tend to cause differences in morphology and behavior and, consequently, differences in classification between adults and larvae. For example, all three species of *Stator* probably have similar larvae because the eggs of all three species are glued tightly to seeds and the larvae enter the seeds directly. Conversely, there is a greater amount of variation in larvae of species of *Acanthoscelides* and *Mimosestes* probably because of differences in methods of attaching eggs and quality of seeds and pods used as hosts. *Stator* has become highly specialized and very successful, whereas species in other genera have apparently evolved different structures in radiating into different niches.

Although the principal thrust of this research was not to evaluate congruence between adult and larval characters, an analysis of our results tends to agree generally with

those of Rohlf (*1963*), because we also have concluded that, although larval and adult interrelationships generally agree, classifications also differ distinctly.

PRINCIPAL COMPONENT ANALYSIS

After the classification presented on page 10 was constructed, a PCA was run to measure differences and similarities between "intuitive" and numerical classifications. The results of the PCA are presented in figure 44. Variables used in the PCA were:

1. Number of teeth on posterior arm of prothoracic plate.
2. Number of teeth on median arm of prothoracic plate.
3. Number of setal pairs associated with prothoracic plate.
4. Number of segments in leg.
5. Number of anal lobes.
6. Number of prothoracic setae, exclusive of those associated with prothoracic plate.
7. Number of primary setae on mesothoracic epipleuron.
8. Number of primary setae on metathoracic prodorsum.
9. Number of secondary setae on postdorsum of abdominal segments 3–5.
10. Number of setae on abdominal segment 10.
11. Number of setae on postdorsum of abdominal segment 9.
12. Number of secondary setae on spiracular area of abdominal segment 1.
13. Number of setae on sternum of abdominal segment 1.
14. Number of secondary setae on prodorsum of abdominal segment 2.
15. Number of primary setae on abdominal epipleuron 8.
16. Number of setae on sternum of metathorax.
17. Number of setae on metathoracic hypopleuron.
18. Number of setae on postdorsum of abdominal segment 8.
19. Number of primary setae on abdominal hypopleuron 3.
20. Number of primary hypopleural setae on mesothorax.
21. Number of secondary setae on prodorsum of abdominal segment 7.
22. Number of secondary setae on abdominal epipleuron 8.

According to Sneath and Sokal (*1973*), three eigenvectors can often represent the majority of the variation among operational taxonomic units (OTU's). This is indicated among the OTU's in this study, for the majority (57 percent) of the distribution can be explained by the three eigenvectors and their eigenvalues. The first component accounts for 24 percent of the total variance. Components 2 and 3 account for progressively less variation—22 percent and 11 percent, respectively, of the total variation.

A three-component plot (fig. 44) illustrates the phenetic relationships between OTU's.

The numerical results of the PCA, including eigenvalues, cumulative proportion of total variance, eigenvectors, and values for each variable may be obtained from the authors by request.

COMPARISON BETWEEN INTUITIVE AND NUMERICAL CLASSIFICATIONS

The results of the PCA (fig. 44) are generally similar to the results obtained using an intuitive approach (see list on p. 10). *Caryobruchus gleditsiae* (Pachymerinae) and *Amblycerus acapulcensis* (Amblycerinae) did not cluster together or with any other groups as would be expected (fig. 44). What was probably most instructive was that *Mimosestes protractus*,

Stator limbatus, S. pruininus, S. pygidialis, and *Zabrotes subfasciatus* clustered at such a great distance from the other species. These five species were classified close to each other in the list on page 10 so both classifications are similar in this respect.

The other cluster in figure 44 is composed of groups 3, 4, and 5. The major differences between the PCA results and the results of the inituitive approach in this cluster are with *Mimosestes amicus* (No. 12), *Acanthoscelides prosopoides* (No. 8), and *Sennius morosus* (No.

16). *M. amicus* clusters very close to *Acanthoscelides aureolus,* with results quite different from our "intuitive" groups (p. 10).

A. prosopoides is somewhat distant from other members of group 3 when subjected to the PCA. *S. morosus* is rather distant from others in the cluster, not matching results in our "intuitive" groups (p. 10). It was pointed out earlier, however, that *S. morosus* was not very closely related to other species in the study, so this is not especially surprising.

GENERAL DESCRIPTION OF FIRST INSTAR BRUCHID LARVAE

The following description is adapted from Prevett (*1971*). Parenthetical comments are ours.

Form: (fig. 1) (cyphosomatic) . . . with thoracic segments larger than those of abdomen; (abdominal segments tapering to a minute tenth segment); cuticle white or yellowish, not sclerotized except on (8th and 9th abdominal tergites in *Acanthoscelides obtectus*) . . ., dorsum of prothorax . . . with scelortized, usually (H-shaped prothoracic) plate; cuticle . . . bearing well defined series of long and short setae, designated primary and secondary setae (respectively).

Head: deeply retracted into prothorax, elongate oval, occipital foramen very large, ventral, divided at about anterior third by tentorial bridge, often uniformly sclerotized, . . . frontal and (coronal) sutures distinct, frons bearing four pairs of setae and, usually, a pair of median sensillae, vertex without setae, sometimes with a pair of dorsolateral sensillae; *antenna* (fig. 23, *P*) completely enclosed by frontal piece, two-segmented, (quadrate basal segment supporting one or more short, stout spines and conical sensillae; distal segment deeply cleft, forming two elongate lobes, long, tactile seta at distal end of shorter lobe); one pair of *ocelli*; *clypeus* (fig. 23, *Q*) largely (sclerotized) . . ., bearing one or two setae and, usually, a sensillum on either side; *labrum* (fig. 23, *Q*) usually narrower than clypeus . . . (distal end broadly ovate; two to five broad setae with anteriorly deflected tips alined near distal end; centered behind, and, on occasions, within an arc of the previous setae, are

two elongate, pointed, sensory setae; one pair of elongate, pointed, sensory setae near mediolateral and proximolateral border; sensory pore located mesad of proximal setal pair); *epipharynx* bearing many fine lateral setae extending from tormae to front margin, diverging in front, two pairs of centrally placed stout setae and, sometimes, a long seta on either side, situated among fine lateral setae towards front margin; *mandibles* heavily sclerotized, normally short, simple, with rounded distal edge, cutting edge gouge-like, mola absent; *maxilla* with small cardo, well-developed stipes and palpifer which bears a one- to three-segmented maxillary palp and single, outer, mala, cardo sometimes bearing a seta, stipes with variable number of long setae on membranous area and sometimes a minute seta on sclerotized ring near insertion of palpifer, palpifer bearing variable number of setae on membranous area or one or two setae on *sclerotized* ring, palp with up to four associated setae . . .; *labium* (fig. 23, *R*) (composed of fused submentum and mentum; single sclerotized plate, with bifid tip, located medially; one short seta near proximolateral border of plate; one pair of elongate setae located mediolaterally in membranous portion of labium).

Thorax: membranous, except for a sclerotized (H-shaped plate with) . . . backwardly projecting teeth on (median and) posterior (arms: fig. 1, *A*); mesothorax and metathorax larger in circumference than prothorax and with tergum divided into two folds (prodorsum and postdorsum); epipleura

(and hypopleura) distinct and swollen; sterna undivided; (swollen lobelike elevations located mesad of thoracic appendages; lobes bearing setae and pointed sclerotized plates; mesothoracic spiracle on epipleuron or hypopleuron near mesoprothoracic border).

Legs: usually present (if absent, replaced by short, pointed seta) composed of (two to three) segments, anterior pair of legs inserted closely together, second and third pairs successively more widely separated (may be of subequal or varying lengths and terminate in a tarsal complex).

Abdomen: membranous; segments 1–(9) with two tergal folds (fig. 1) (pro- and postdorsum); (epipleura and hypopleura distinct); sterna undivided, bearing many backwardly directed minute spines . . .; spiracles situated (in dorsoanterior aspects of epipleuron) of segments 1–8; segment 9 (reduced); segment 10 minute, nipple-shaped, divided into two or three equal lobes by transverse or Y-shaped anal sulcus; segment one bearing a strongly sclerotized (posteriorly directed) spine close to spiracle.

Spiracles: . . . unicameral or bicameral. . . .

Tracheal system: with 4–13 pairs of enlarged chambers in the main branches.

KEY TO SOME SPECIES OF FIRST INSTAR BRUCHID LARVAE

1. Legs and primary setae absent 2
   Legs and primary setae present 6
2(1). Elongate, pointed, median tooth on posterior arm of prothoracic plate (fig. 22, S) 3
   Posterior arm of prothoracic plate lacking a median, elongate, pointed tooth . . 5
3(2). Without setae on hypopleuron of meso- and metathorax 4
   Seta (*h*) on hypopleuron of meso- and metathorax (fig. 19) . . . .*Stator pruininus* (Horn)
4(3). Setae *u* and *v* on sternum of mesothorax through abdominal segment 7; thoracic appendages replaced by lateral lobes (fig. 20); egg with prominent anterior, middorsal point (fig. 45, 4) . . . .
   . . . .*Stator pygidialis* (Schaeffer)
   Setae *u* and *v* absent on sternum of meso- and metathorax; seta *u* absent on abdominal sterna 1–7; thoracic appendages replaced by seta *K*, lateral lobes absent; egg convex dorsally . . . .
   . . . .*Stator limbatus* (Horn)
5(2). Prothoracic plate with posterior, median, and anterior arms; five pairs of setae on prothorax . . . .
   . . . .*Mimosestes protractus* (Horn)
   Prothoracic plate vestigial, composed of two sclerotized teeth projecting above integument (fig. 22, *T*); 15 pairs of setae on prothorax . . . .
   . . . . . .*Zabrôtes subfasciatus* (Boheman)

6(1). Segment 10 with transverse anal aperture 7
   Segment 10 with Y-shaped anal aperture 19
7(6). Legs of subequal lengths 8
   Each pair of legs slightly longer than preceding pair or meso- and metathoracic legs subequal in length and prothoracic legs greatly reduced in length (*A. baboquivari*; fig. 23, *B*) 12
8(7). Legs bearing a rounded tarsal complex (fig. 23, *N*) 9
   Legs bearing a flattened tarsal complex (fig. 23, *L*); large, median tooth on posterior arms of prothoracic plate; few prothoracic setae; first abdominal sternum lacking setae; ninth abdominal epi- and hypopleuron bare . . . .
   . . . .*Mimosestes amicus* (Horn)
9(8). Setae *u*, *v*, or *x* on sternum of abdominal segments 1–9; seta *A* on postdorsum of abdominal segment 6; sclerotized plates on abdominal sterna reduced in size 10
   Abdominal sterna without setae and possessing numerous, enlarged sclerotized plates; seta *A* absent on abdominal segment 6; seta *E* very short on abdominal segment 6; three setae on distal portion of proximal leg segment of meso- and metathorax; seta 17 on prothorax . . . . . .
   . . . .*Sennius morosus* (Sharp)
10(9). Hyposternal setae absent on meso-

and metathorax (fig. 6); seta *h* on abdominal segment 9 11

Hyposternal setae on meso- and metathorax (fig. 4); seta *h* absent on abdominal segment 9; dorsum of mesothoracic and metathoracic segments lacking primary setae ....
..... *Acanthoscelides chiricahuae* (Fall)

11(10). Paired setae at base of thoracic appendages (fig. 23, *E*); median arm of prothoracic plate bearing two teeth; seta *A* on abdominal segment 1; seta *a″* on abdominal segment 2; seta *e′* absent on abdominal segments 2–4; seta *a′* on abdominal segment 8; seta *a″* on abdominal segment 9 ....
...... *Acanthoscelides macrophthalmus* (Schaeffer)

Paired setae absent at base of thoracic appendages (fig. 23, *N*); median arm of prothoracic plate bearing three or more teeth; seta *A* absent on first abdominal segment; seta *d′* and *d″* on prodorsum of abdominal segment 7; secondary setae absent on postdorsum of abdominal segment 2; seta *E* absent on abdominal segments 2–4 ....
..... *Neltumius arizonensis* (Schaeffer)

12(7). Each pair of legs slightly longer than preceding pair; median arm of prothoracic plate with two or more teeth, if only one tooth on median arm then posterior arm with more than three teeth; seta *f* not on sternum of meso- and metathorax 13

Mesothoracic and metathoracic legs subequal in length, prothoracic legs very short; median arm of prothoracic plate with one tooth, posterior arm with three teeth and not expanded laterally; seta *f* on meso- and metasternum; thoracic sterna without sclerotized plates; only seta *g* on abdominal segment 10 ....
.. *Acanthoscelides baboquivari* Johnson

13(12). Median arm of prothoracic plate with three teeth, posterior arm with three or fewer teeth 14

Median arm with fewer than three teeth, posterior arm with more than three teeth 15

14(13). Seta *d′* on abdominal prodorsum 8; seta *a′* on postdorsum of abdominal segment 9; seta *E* on epipleuron of abdominal segment 9; secondary seta *h* only on abdominal hypopleuron 9 ....
.... *Acanthoscelides aureolus* (Horn)

Seta *d′* absent on abdominal prodorsum 8; seta *a′* lacking on postdorsum of abdominal segment 9; seta *E* absent on epipleuron of abdominal segment 9; primary seta *H* on abdominal hypopleuron 9
.... *Acanthoscelides mixtus* (Horn)

15(13). Median arm of prothoracic plate with two teeth 16

Median arm of prothoracic plate with one tooth 18

16(15). Prodorsum cf abdominal segments lacking primary seta *D*; hypopleuron of abdominal segments 1–9 with secondary setae only; setae *a′* and *a″* on postdorsum of abdominal segment 9 17

Primary seta *D* on prodorsum of abdominal segments 2–7; hypopleuron of abdominal segments 1–8 with primary seta *H*; secondary setae *a′* and *a″* lacking on postdorsum of abdominal segment 9; setae *d′* and *d″* on prodorsum of abdominal segment 8; setae *a′* and *a″* on postdorsum of abdominal segments 1–7 ....
Acanthoscelides prosopoides (Schaeffer)

17(16). Median tooth on posterior arm of prothoracic plate elongate and pointed apically; primary seta *A* on postdorsum of abdominal segment 1; spiracular seta *s′* on abdominal segment 1; seta 17 absent on prothoracic sternum ....
.... *Mimosestes sallaei* (Sharp)

Teeth on posterior arm of prothoracic plate similar in size; only secondary seta *a′* on postdorsum of first abdominal segment; spiracular seta *s′* absent; seta 17 on prothoracic sternum; seta *A* on abdominal postdorsum 9, at least six times longer than seta *a′* ....
.... *Acanthoscelides collusus* (Fall)

18(15). Sclerotized plate on dorsum of abdominal segments 8 and 9; setae *s′*, *d′*, and *A* on abdominal segment; spiracle on hypopleuron of mesothorax; setae located distally on basal leg segment appear elongate and decurved (fig. 23, *G*) .
.... *Acanthoscelides obtectus* (Say)

Schlerotized plates lacking; only seta *a′* on dorsum of abdominal segment 1; spiracle in epipleuron of mesothorax; distal setae on basal leg segment greatly

reduced (fig. 23, *I*); hypopleuron of abdominal segment 1 with seta *h* ....
........*Albarobius prosopis* (LeConte)
19(6). Apical end of distal leg segment with well developed, immobile claw (fig. 23, *K*); leg segments lacking internal sclerotized plates; six pairs of setae between halves of prothoracic plate; prothoracic plate lacking median arms; setae *Bb'b"* on abdominal segments 2–7

....*Caryobruchus gleditsiae* (Linnaeus)
Distal leg segment with elongate, fleshy lobe with opposable, flexible, sclerotized claw (fig. 23, *J*); internal sclerotized plates evident in leg segments; five pairs of setae between halves of prothoracic plate; prothoracic plate with median arms; abdominal segment 10 with setae *a'*, *A*, and *h* ....
.. *Amblycerus acapulcensis* Kingsolver

DESCRIPTIONS AND DISCUSSIONS OF LARVAE

Acanthoscelides aureolus (Horn)

Summary of chaetotaxy: Table 1.[4]
Prothorax (fig. 2).—With 10 setae, exclusive of those associated with prothoracic plate (fig. 22, *A*); seta 12 on elevated portion of integument; sternum with few sclerotized plates.
Prothoracic plate (fig. 22, A).—Median and posterior arms with three teeth; posterior arm with lateral extension; seta 2 (fig. 22, *C*) located medially; seta 5 and associated sensory pore on mesal border of posterior arm.
Mesothorax and metathorax (fig. 2).—Prodorsum with one seta (*d"*). Postdorsum with one primary (*A*) and one secondary (*a"*) setae. Mesoepipleuron with two setae (*E, e'*); metepipleuron with single secondary seta. Hypopleuron lacking setae; spiracle on mesohypopleuron. Sternum with two setae (*u, R*); few sclerotized plates.
Legs (fig. 23, A).—Two-segmented; each pair longer than preceding pair; distal end of second segment with flattened tarsus; pair of tactile setae at apical end of basal segment; pair of sensory pores at base of meso- and metathoracic appendages; single sensory pore at base of prothoracic appendage.
Abdomen (fig. 24).—Prodorsa of segments 1–8 with seta *d'* only; prodorsum 9 lacking setae. Postdorsum of segment 1 with one seta (*a'*); postdorsa 2–8 with primary and secondary (*a"*) setae; postdorsum 9 with one primary (*A*) and two secondary (*a', a"*) setae. Dorsum of segment 10 with seta *g*. Spiracular area without setae; spine on segment 1. Epipleuron of segments 1 and 9 with primary setae only;

segment 2 with seta *e'* only; remaining epipleura 3–8 with two setae (*E, e'*). Hypopleuron of segments 1–9 with single seta (*h*); hypopleuron 10 bare. Sternum of segments 1, 3, and 8 with two setae (*v, x*); segments 2 and 4–7 with three setae (*u, v,* and *x*); single seta on segments 9 (*v*) and 10 (*x*). Segment 10 with transverse anal aperture.
Significant characters.—Each pair of legs slightly longer than preceding pair; median and posterior arms of prothoracic plate with three teeth; seta *d'* on abdominal prodorsum 8; seta *a'* on postdorsum of abdominal segment 9; seta *E* on abdominal epipleuron 9; only seta *h* on abdominal hypopleuron 9.
Specimens examined.—30.
Host plants.—*Astragalus praelongus* Sheldon: Arizona. Coconino Co.: 6 mi SW Tuba City (Moenave Reservoir), 7 August 1971. Yavapai Co.: Junction of Tuzigoot Natl. Mon. and Hwy. 89, 27 May 1971, 27 June 1971, 17 July 1971.[5]
Glycyrrhiza lepidota (Nutt.): Arizona. Coconino Co.: 6 mi SW Tuba City (Moenave Reservoir), 19 June 1971.
Biological notes.—Larvae were collected from the seeds of *G. lepidota* (Nutt.), but about 95 percent were from *Astragalus praelongus* Sheldon. The pods of *A. praelongus* possess thick walls that are fleshy when immature and become woody upon maturation (Kearney and Peebles, *1969*). The pods are only partially dehiscent, and many seeds are retained within the dehisced pod. Bruchid females apparently enter the partially dehisced pod and oviposit one to several eggs on each seed. The eggs are secured to the seed surface by a broad,

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[4]All tables appear in the Appendix, beginning on p. 69.

[5]Seeds were collected by G. S. Pfaffenberger unless otherwise designated.

peripheral band of mucilage, which is much wider at the broad or anterior end of the egg. This is perhaps necessary to increase the resistance needed by the larva as it probably relies upon the egg chorion for purchase in boring into the seed.

Acanthoscelides aureolus does not appear to prefer any particular stage of seed development because first instars were obtained from seeds in which initial cotyledon development had not occurred. However, most of the larvae were collected from fully mature seeds. Females appear to be consistent as to where they oviposit the eggs (fig. 45, 1*D*).

After entering the seed, the first instar burrows the short distance through the cotyledon and into the seedcoat tissue (fig. 45, 1*E*). The larva feeds on this tissue throughout the first and part of the second instars, then it begins to feed on the cotyledons. The larva, with its dorsum resting on seedcoat tissue and its venter facing the cotyledons, feeds in semicircular movements. The larva devours the seed leaf tissue until contact is made with the seed integument (fig. 45, 1*A*). Usually, when this happens, only the small end fragments of the cotyledons remain (fig. 45, 1*C*), and packed tightly at one end of the chamber formed by feeding are exuviae, which have been shed at previous molts.

The larva is usually in the latter stages of the fourth instar when the cotyledons have been consumed. It then gnaws a circular groove on the inside of the seed integument, forming a concentric line of weakness around an operculum. The larva then rotates 180°, coming to rest with its venter upon the remnants of the seedcoat tissue. The prepupal molt occurs within this chamber. After molting, the adult finishes chewing around the operculum and pushes it outward, leaving a hole through which the adult emerges.

Although numerous seeds were found with several eggs and larval entry holes on their surfaces, when the seed contents were examined only one larva could be found. Cannibalism apparently occurs because we observed a late instar larva consuming an earlier instar.

Discussion.—*A. aureolus* is more closely related to *A. mixtus* than to other members of the complex (see discussion of *A. baboquivari*). Their prothoracic plates are identical (except for a slight posterolateral extension of the posterior arms of *A. aureolus*), and both species infest closely related host plants (*A. aureolus* infests *Astragalus praelongus* and *A. mixtus* infests *Astragalus wootoni*).

These two species are easily distinguished by the setae A, a', a" on the postdorsum of abdominal segment 9, and the secondary seta on abdominal hypopleuron 9, of *A. aureolus* (primary seta (*H*) on abdominal hypopleuron 9, of *A. mixtus*) (figs. 24 and 29).

Because of similarities of the prothoracic plates of *A. aureolus* and *A. mixtus* to Kunhikannan's (*1923*) drawing of "*Mylabris nigrinus*," we feel that he had misidentified specimens of Bruchidae and that he actually studied either one or both of these species of *Acanthoscelides*. This is even more probable because "*M. nigrinus*" is known to feed only in the seeds of *Cassia*, not *Astragalus* (Johnson and Kingsolver, *1973*).

For additional distinguishing characters of *A. aureolus*, see the characters in the key (p. 20).

Acanthoscelides baboquivari Johnson

Summary of chaetotaxy: Table 2.

Prothorax (fig. 3).—With 10 setae, exclusive of those associated with prothoracic plate (fig. 22, *B*); sternum lacking sclerotized plates.

Prothoracic plate (fig. 22, B).—Median arm with one tooth, posterior arm with three teeth; median and posterior arms short, anterior arms elongate; seta 5 (fig. 22, *C*) and sensory pore on posterior arm near mesal border.

Mesothorax and metathorax.—Prodorsum without setae. Postdorsum with three setae (A, a', a"). Mesoepipleuron with primary (*E*) and secondary (*e'*); single seta (*e'*) on metepipleuron. Hypopleuron lacking setae; spiracle on mesohypopleuron. Sternum with three setae (*u, f, R*); sclerotized plates absent.

Legs (fig. 23, B).—Two-segmented; mesothoracic and metathoracic appendages subequal in length, prothoracic appendages greatly reduced in length; distal end of second segment with rounded tarsus; pair of tactile setae at distal end of basal segment; pair of

sensory pores located basally on proximal segment.

Abdomen (fig. 25).—Prodorsum of segments 1–8 with single seta (*d'*); prodorsum 9 without seta(e). Postdorsum of segments 1–8 with primary and secondary (*a''*) setae; postdorsum 9 with one primary (*A*) and two secondary (*a'*, *a''*) setae. Dorsum of segment 10 with seta *g*. Spiracular area of segment 8 with numerous small elevations; setae absent; spine on segment 1. Hypopleuron of segments 1–9 with one seta (*h*); hypopleuron 10 without setae. Sternum of segments 1–8 with two setae; one seta (*v*) on sternum 9; sternum 10 without setae; sclerotized plates absent. Segment 10 with transverse anal aperture.

Significant characters.—Meso- and metathoracic legs subequal in length, prothoracic legs greatly reduced in length; median arm of prothoracic plate with one tooth, posterior arm with three teeth, not laterally expanded; seta *f* on meso- and metasternum; sclerotized plates absent on thoracic sterna.

Specimens examined.—11.

Host plants.—*Indigofera sphaerocarpa* Gray: Arizona. Pima Co.: Kitt Peak, 5 October 1972. Cochise Co.: Miller Cyn., Huachuca Mts., 6 October 1972 (both C. D. Johnson).

Biological notes.—For information concerning ecology and behavior, see Johnson (*1974*).

Discussion.—We recognize *Acanthoscelides baboquivari* as a species belonging to a group that includes *A. aureolus*, *A. mixtus*, *A. collusus*, *A. prosopoides*, *A. obtectus*, and *Algarobius prosopis*. These species share: (1) 8 to 10 pairs of setae on the prothorax, exclusive of those associated with the prothoracic plate; (2) the gross morphology of the prothoracic plate and associated setal arrangement are similar; (3) bare hypopleural regions of meso- and metathorax (except *A. prosopoides*), setae (*H*, *h*) on mesohypopleuron; (4) each pair of legs longer than preceding pair (except *A. baboquivari*) each possessing a pair of tactile setae at distal end of basal leg segment; (5) absence of seta *s'* (except *A. obtectus*, first abdominal segment); (6) epipleural chaetotaxy of thorax and abdomen (setae *E* and *e'* absent on mesoepipleuron of *A. prosopoides*), seta *E* absent on abdominal segment 9 of *A. mixtus*; and (7) hypopleuron 10 either absent (*A. obtectus*) or without setae.

On the basis of larval morphology and behavior and ovipositional behavior, we have divided this group into two subgroups. What we consider to be the more advanced subgroup includes *A. baboquivari*, *A. aureolus*, *A. mixtus*, and *A. collusus*. In this subgroup, the gross morphology of the prothoracic plate is quite similar as is the hypopleural chaetotaxy (primary setae absent) and numbers of setal pairs (10 pairs, excluding those associated with prothoracic plate) on the prothorax. *A. mixtus* differs slightly by possessing seta *H* on abdominal segment 9 and nine pairs of setae on the prothorax, other than those associated with the prothoracic plate. The larvae of these species are the only members of the complex to enter the pod or seed upon eclosion. According to Center,[6] *A. collusus* may wander over the pod surface of *Errazurizia rotundata* before penetration, behavior typical of members of the other subgroup. Egg-laying behavior of adults of the first subgroup probably represents a more advanced condition (Bridwell, *1918*; Center and Johnson, *1974*; Zacher, *1930*) in that the eggs are cemented to the pod or seed surface.

Members of the second subgroup (*Acanthoscelides prosopoides*, *A. obtectus*, and *Algarobius prosopis*) differ from the first subgroup in that they either possess or express a number of what we consider to be primitive characters. The secondary hypopleural setae of the first group have mostly been replaced by primary setae (abdominal segments 1–9, except the first segment of *A. prosopis*). The primary setae are of greater length than those of the first subgroup. Moreover, the eggs are not cemented to the pod or seed surface as they are in the first subgroup, and the first instar wanders over the pod or seed surface after eclosion and before penetration. The eggs of *A. prosopoides* are cemented only near the center, whereas the ends remain unattached (Forister and Johnson, *1971*). This may represent a transitional form of egg-laying behavior intermediate to that of the first subgroup and

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[6] CENTER, T. D. A SURVEY OF SOME LEGUME SEED-FEEDING INSECTS OF NORTHERN ARIZONA WITH NOTES ON THE LIFE HISTORIES OF THE BRUCHIDAE(COLEOPTERA). Unpub. Master's thesis. Northern Arizona University. 157 pp. 1971.

that of the remaining members of the second subgroup. The ovipositional behavior of *Acanthoscelides obtectus* and *Algarobius prosopis* is thought to be most primitive (Bridwell, *1918*) because the eggs are not cemented but are oviposited in cracks, crevices, or holes in the pod or seed surface (Center and Johnson, *1974*; Zacher, *1930*).

First instars of *Acanthoscelides baboquivari* are easily recognized by the arrangement of the teeth on the prothoracic plate (one tooth on each median arm and three teeth on each posterior arm). The only other members of this complex to possess a single tooth on each median arm (*Acanthoscelides obtectus* and *Algarobius prosopis*) belong to the second subgroup. *A. baboquivari* can be easily separated from these species by relative length of primary setae, development of legs, and number of teeth appearing on posterior arm of prothoracic plate.

Acanthoscelides chiricahuae (Fall)

Summary of chaetotaxy: Table 3.

Prothorax (fig. 4).—With nine setae, excluding those associated with prothoracic plate (fig. 22, *C*); three horizontal rows of sclerotized plates on sternum.

Prothoracic plate (fig. 22, C).—Median arms with two or three teeth; posterior arms with four irregularly shaped teeth; seta 5 (fig. 22, *C*) on median border of posterior arm; distal end of posterior arm with slight lateral expansion; seta 2 (fig. 22, *C*) in line with setae 1 and 3; anterior arms narrow and elongate.

Mesothorax and metathorax (fig. 4).—Prodorsum lacking setae. Postdorsum with single seta (*a"*). Epipleuron with two setae (*E*, *e'*). Mesohypopleuron with one seta (*H*) and spiracle; several bumps on anterodorsal border of spiracle; metahypopleuron with primary and secondary (*h*) setae. Sternum with two setae (*u*, *R*); numerous, irregular rows of sclerotized plates.

Legs (fig. 23, C).—Two-segmented, subequal in length; apical end of distal segment forming rounded tarsus; pair of tactile setae located distally on basal segment.

Abdomen (fig. 26).—Prodorsum of segments 1–9 with single seta (*d'*); seta *d'* on segments 1–5 with closely associated sensory pore. Post-

dorsum of segment 1 with primary (*A*) and two secondary (*a'*, *a"*) setae *A*, *a"* closely associated, near tergo-pleural border; segments 2–9 with two setae (*A*, *a"*). Dorsum of segment 10 with seta *g*. Spiracular areas lacking setae; spine on first segment. Epipleuron of segments 1 and 9 with primary setae only; segments 2–5 with secondary setae only; segments 6–8 with primary (*E*) and secondary (*e'*) setae. Hypopleuron of segments 1–8 with seta *h* only; hypopleura 9 and 10 bare. Sternum of segments 1 (*u*, *x*), 2–5 (*u*, *v*), and 9 (*u*,*v*) with two setae; segments 6–8 and 10 with seta *u*; numerous sclerotized plates on segments 1–8. Segment 10 with transverse anal aperture.

Significant characters.—Legs of subequal length and possessing a rounded tarsal complex; setae *u*, *v*, or *x* on sternum of abdominal segments 1–9; seta *A* on postdorsum of abdominal segment 6; hyposternal setae on meso- and metathorax.

Specimens examined.—6.

Host plants.—*Mimosa biuncifera* Benth.: Arizona. Yavapai Co.: Verde Valley, fall 1972 (G. W. Forister).

Biological notes.—See Forister[7] for information on behavior of adult and first instar, egg characteristics, developmental time, and parasitism. As reported by Forister (*1970*), it was not uncommon to observe eclosion through the dorsoanterior end of the chorion.

The mucilage used to cement the egg to the pod surface or seed test appeared either as a broad band or as filaments encircling the egg. On numerous occasions, we observed several to many eggs glued together in a single mass on the seed surface.

The first instar most commonly began feeding on or near the hypocotyl, then it began consuming the cotyledons. The entire contents of the seed were consumed before pupation occurred. The adult escaped through a small circular exit hole in the side of the seed.

Discussion.—*Acanthoscelides chiricahuae* resembles *Neltumius arizonensis* because both species possess legs of subequal lengths, and the tip of the distal segment is rounded. Also, upon eclosion, both species may bore di-

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[7] FORISTER, G. W. BIONOMICS AND ECOLOGY OF 11 SPECIES OF BRUCHIDAE (COLEOPTERA). Unpub. Master's thesis. Northern Arizona University. 93 pp. 1970.

rectly into the pod from the egg or they may exit through the anterior end of the egg and crawl beneath the egg chorion, using it as a brace. The ability to behave both ways is unique to these two species. Usually, however, both species bore directly into the seed from the egg.

A. chiricahuae possesses a prothoracic plate with a distinct shape (fig. 22, *C*) and also differs remarkably in its chaetotaxy from *N. arizonensis. Mimosa biuncifera*, the host plant of this species, is also different from the host plant of *N. arizonensis*. Because of these fundamental differences, we feel that *A. chiricahuae* occupies a distinct phylogenetic group.

Although the drawings of the prothoracic plate of "*Mylabris pauperculus*" by Kunhikannan (*1923*) are not as detailed as ours, it is very likely that he dealt with *A. chiricahuae*, not *A. pauperculus*. We believe this to be true because of the obvious similarities in the prothoracic plates and because *Mimosa biuncifera* is not known to be a host of *A. pauperculus* (Johnson, *1970*).

Acanthoscelides collusus (Fall)

Summary of chaetotaxy: Table 4.

Prothorax (fig. 5).—With 10 setae exclusive of those associated with the prothoracic plate (fig. 22, *D*); sternum with sclerotized plates of differing sizes; smaller plates scarce, located anteriorly; larger plates more numerous, located medially on sternum.

Prothoracic plate (fig. 22, D).—Median arm with two teeth, posterior arm with five teeth; seta 2 (fig. 22, *C*) located centromedially; seta 3 bordering anterior base of median arm; seta 5 and associated sensory pore on medial border of posterior arm; medial border of posterior arm straight, lateral border extended laterally; four pairs of setae between anterior arms.

Mesothorax and metathorax (fig. 5).—Prodorsum with primary (*D*) and two secondary (*d'*, *d"*) setae. Postdorsum lacking setae. Mesoepipleuron with two setae (*E*, *e'*); single seta (*e'*) on metepipleuron. Mesohypopleuron with spiracle; metahypopleuron bare. Sternum with two setae (*u*, *R*); few sclerotized plates.

Legs (fig. 23, D).—Two-segmented, each pair longer than preceding pair; distal segment bearing flattened tarsus; pair of tactile setae at distal end of basal segment; sensory pore between base of tactile setae on mesothoracic appendage; pair of sensory pores at base of each appendage; basal segment of metathoracic appendage with medial sensory pore on anterior margin.

Abdomen (fig. 27).—Prodorsum of segments 1–8 with single seta (*d'*); prodorsum 9 without setae. Postdorsum of segment 1 with seta *a'* only; postdorsa 2–8 with two setae (*A*, *a"*); postdorsum 9 with primary (*A*) and two secondary (*a'*, *a"*) setae. Dorsum of segment 10 with seta *g*. Spiracular areas without setae; spine on segment 1. Epipleuron of segments 1 and 9 with primary setae only; segment 2 with single seta (*e'*); remaining epipleura with two setae (*E*, *e'*). Hypopleuron of segments 1–9 with secondary seta (*h*) only; hypopleuron 10 lacking setae. Sternum of segments 1–7 with three setae; two setae (*v*, *x*) on segment 8; segments 9 and 10 with one seta each (*x* and *v*, respectively); sclerotized plates absent on segment 10, rare on segments 1–6; sclerotized plates more numerous on segments 7–9, appearing in one or two lateral rows. Segment 10 with transverse anal aperture.

Significant characters.—Each pair of legs exceeding length of preceding pair, tarsal complex flattened; seta *D* absent on abdominal prodorsa; hypopleuron of segments 1–9 with secondary setae only; abdominal postdorsum 9 with two secondary setae (*a'*, *a"*); teeth on posterior arm of prothoracic plate similar in size and shape; only seta *a'* on first abdominal postdorsum; spiracular seta (*s'*) absent.

Specimens examined.—32.

Host plants.—*Parryella filifolia* Torr. and Gray: Arizona. Coconino Co.: 6 mi SW Tuba City (Moenave Reservoir), 7 August 1971.

Biological notes.—Bionomics, host plants, developmental period, percentage infestation, and possible evolution of traits by the plant to avoid predator satiation are discussed by Center.[8] We found a marked preference by the first and early second instars for the endosperm tissue. After seed penetration, the larva feeds

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[8] See footnote 6.

upon and moves through the endosperm. During the latter part of the second stadium, the larva begins feeding on the cotyledons. The larva gnaws a circular hole in the center of one cotyledon before feeding on the second cotyledon. Occasionally, two and sometimes three larvae were found within the same seed. Because only one adult usually emerges from a seed, cannibalism probably occurs.

Discussion.—The prothoracic plates of *Acanthoscelides collusus* and *A. prosopoides* (fig. 22,*H*) are more similar to each other than to other members of the complex mentioned in the discussion of *A. baboquivari*. The arrangement of teeth on the prothoracic plate is similar as is the arrangement of the associated setae. *A. collusus* possesses two more pairs of setae on the prothorax and only secondary setae on the hypopleural regions of the abdominal segments. They also differ in their larval and egg-laying behavior (see discussion of *A. baboquivari*).

The species treated as *"Mylabris horni"* by Kunhikannan (*1923*) may actually have been *Acanthoscelides collusus*. There is a distinct resemblance between the prothoracic plates, and *A. collusus* is known to feed in *Amorpha fruticosa*, the seeds from which Kunhikannan reared his specimens. *"M. horni"* is now a synonym of *Acanthoscelides submuticus* (Sharp) (Johnson, *1970*). Unfortunately, we were unable to obtain specimens of *A. submuticus*, a species that also feeds in *Amorpha fruticosa*.

Acanthoscelides macrophthalmus (Schaeffer)

Summary of chaetotaxy: Table 5.

Prothorax (fig. 6).—With nine setae, exclusive of those associated with prothoracic plate (fig. 22,*E*); sternum lacking sclerotized plates.

Prothoracic plate (fig. 22, E).—Median arms with two teeth; broad posterior arms with seven teeth, median tooth elongate, remaining teeth of subequal size; seta 2 (fig. 22, *C*) located medially; seta 5 within plate of posterior arm; laterodistal area of posterior arm extended laterally.

Mesothorax and metathorax (fig. 6).—Prodorsum with primary (*D*) and two secondary (*d'*, *d"*) setae; sensory pore closely as-

sociated with seta *d'*. Postdorsum without setae. Mesoepipleuron with two setae (*E, e'*); single seta (*e'*) on metepipleuron. Hypopleuron lacking setae; spiracle on mesohypopleuron. Sternum of mesothorax with two setae (*U, R*); metasternum with one seta (*R*); sclerotized plates of different types, sizes, and distributions.

Legs (fig. 23, E).—Two-segmented; subequal in size; apical end of distal segment forming rounded tarsus; pair of tactile setae at proximal end of basal segment; first and third appendage pairs with pair of tactile setae at distal end of basal segment; second appendage pair with one seta at apical end of basal segment.

Abdomen (fig. 28).—Prodorsum of segments 1 through 7 with single seta (*d'*); seta *d'* with closely associated sensory pore on segments 1-5; prodorsa 8 and 9 without setae. Postdorsum of segment one with single seta (*A*); setae *A, a"* on segments 2-7; postdorsum of segments 8 and 9 with three setae (*A, a', a"*). Dorsum of segment 10 with seta *g*. Spiracular area of segments 2-8 with small, pointed, sclerotized projections; seta *s'* at base of spine on segment 1. Epipleuron of segments 1 and 9 with seta *E* only; segments 2-4 without setae; remaining segments 5-8 with two (*E, e'*) setae. Hypopleuron of segments 1-10 with one secondary seta. Sternum of segments 1-8 with three setae (*u, v, x*); seta *v* on sternum 9; setae lacking on segment 10; numerous sclerotized plates on all sterna; plates appear larger on segments 1-4 and 10 than on remaining sterna. Segment 10 with transverse anal aperture.

Significant characters.—Legs of subequal length and possessing rounded tarsal complex; median arm of prothoracic plate with two teeth; only seta *A* on first abdominal postdorsum; single, elongate tooth on median edge of posterior arms of prothoracic plate.

Specimens examined.—26.

Host plants.—*Leucaena glauca* (Linnaeus): Mexico: 2 mi SW Guaymas, Sonora, 13 March 1973 (C. D. Johnson).

Biological notes.—The oval eggs are usually laid individually upon the surface of the pod. They are cemented to the pod surface by what appears to be partially fused, elongate strands of mucilage. These strands are longer and

most highly concentrated at the anterior or enlarged end of the egg and only a few, short strands appear at the posterior end. The middle of the egg appears to be nearly devoid of these strands. On numerous occasions, we observed clusters of eggs in old exit holes.

The first instar penetrates the pod directly from the egg and consumes the entire contents of a single seed.

Discussion.—We consider *Acanthoscelides macrophthalmus* to be a member of a group that includes *Mimosestes amicus* and *M. sallaei*. In all three species, the prothoracic plates and associated setal arrangements are similar; all possess two teeth on the median arms and an elongate, pointed, median tooth subtended by six or seven short, rounded teeth on the posterior arms. The chaetotaxy on the epipleural and hypopleural regions of the mesothorax and metathorax and most abdominal segments, excepting some intrasegmental areas (that is, first abdominal spiracular areas and abdominal epipleura 2–5), is quite similar.

The three species differ, however, in the appearance of their thoracic appendages, host plants, larval behavior, and chaetotaxy of the prothorax (*M. amicus*) and meso- and metathoracic tergites (*A. macrophthalmus*). There is a gradation from primitive to a derived condition in this group in the degree of development of the legs and the appearance of the foot apparatus.

The legs of *A. macrophthalmus* are of subequal lengths, and upon eclosion the first instar bores directly into the pod of *Leucaena glauca*. The first and second pairs of appendages possess a rounded tarsus, whereas the tip of the distal segment of the metathoracic appendages (fig. 23, *E*) appears to represent a morphological condition intermediate of that expressed by the rounded tarsus (figs. 23, *C*; 25, *N* and *O*) and the flattened tarsus of *M. amicus* (fig. 23, *L*). This condition may represent mosaic regression within this species. Thus, this species may likely be in a stage of transition from a species that possesses a flattened tarsus and wanders over the pod or seed surface before entrance (primitive; MacSwain, *1956*) to one that possesses a rounded tarsus and penetrates the pod or seed directly upon eclosion (more advanced).

The legs of *M. amicus* (fig. 23, *L*) are also of subequal lengths but possess a flattened distal tip, which would seem more conducive to locomotion. The first instar most frequently penetrates the pod of *Prosopis juliflora* directly upon eclosion but may also exit through the anterior end of the egg and crawl beneath the egg chorion, using it for purchase. This combination of morphological and behavioral characters probably represents a more primitive condition than that of *A. macrophthalmus*.

The legs of *Mimosestes sallaei* (fig. 23, *M*) are much better developed, being longer, of varying lengths and possessing a flattened tarsus. All of these features apparently contribute to more effective locomotion and pod penetration. This species may burrow directly from the egg into the pod of *Acacia farnesiana* (C. D. Johnson, unpublished data) or other host plants, or it may exit through the anterior end of the egg and walk over the pod surface before penetration (Kunhikannan, *1923*). The advantages associated with legs in which the length of one pair is exceeded by the length of the succeeding pair is best described by Kunhikannan (*1923*) in his description of a primitive species, *Acanthoscelides obtectus*.

Acanthoscelides mixtus (Horn)

Summary of chaetotaxy: Table 6.

Prothorax (fig. 7).—With nine setae, excluding those associated with the prothoracic plate (fig. 22, *F*); sternum with few sclerotized plates.

Prothoracic plate (fig. 22, F).—Median and posterior arms with three teeth; sides of posterior arms subparallel; median arms prominent; seta 2 (fig. 22, *C*) located medially; seta 5 and associated sensory pore located mesad of medial border of posterior arm; length of anterior and posterior arms subequal.

Mesothorax and metathorax (fig. 7).— Prodorsum with one seta (*d'*). Postdorsum with single primary and secondary (*a"*) setae. Mesoepipleuron with two setae (*E, e'*); metepipleuron with one secondary seta (*e'*). Mesohypopleuron asetiferous, spiracle present; metahypopleuron bare. Sternum with two setae (*u, R*); sclerotized plates few and appearing in three rows.

Legs (fig. 23, F).—Two-segmented; each pair

longer than preceding pair; distal segment with flattened tarsus; pair of tactile setae located distally on basal segment; pair of sensory pores appearing proximally on basal segment.

Abdomen (fig. 29).—Prodorsum of segments 1–7 with single seta (d'); remaining prodorsa without setae. Postdorsum of first abdominal segment with single secondary seta (a''); setae A and a' on postdorsum of segments 2–9. Dorsum of segment 10 with seta g. Spiracular area lacking setae, spine on segment 1. Epipleuron of segment 1 with a primary seta; seta e' on segment 2; segments 3–8 with two setae (E, e'); epipleuron 9 without setae. Hypopleuron of segments 1–8 with single seta (h); segment 9 with primary seta only; segment 10 without setae. Sternum of segments 1–7 with three setae (u, v, x); two setae (u, x) on segment 8; segments 9 and 10 with one seta each (v and x, respectively); sclerotized plates sparse, usually in one or two lateral rows. Segment 10 with transverse anal aperture.

Significant characters.—Each pair of legs slightly longer than preceding pair; median and posterior arms of prothoracic plate with three teeth; posterior arms of prothoracic plate not expanded laterally; seta d' absent on abdominal prodorsum 8; abdominal segment 9 lacking seta E on epipleuron and seta a' on postdorsum; seta H on abdominal hypopleuron 9.

Specimens examined.—17.

Host plants.—*Astragalus wootoni* Sheldon: Arizona. Yavapai Co.: 9 mi S Sedona, 19 June 1971, 27 June 1971, 17 July 1971. Junction of Tuzigoot Natl. Mon. and Hwy. 89, 27 May 1971, 19 June 1971, 27 June 1971.

Biological notes.—See Johnson (*1970*) for a list of known host plants. All the larvae used in this study were obtained from the seeds of *A. wootoni* (fig. 45, 2). The pods, when mature, are approximately 20 to 25 mm in length and 10 to 15 mm wide. They possess membranous walls and are indehiscent. The ovules are attached by a funiculus (fig. 45, 2D) to the midrib of the ovary. Because no eggs were observed upon the seeds or within the pod, we assume that the female oviposits upon the pod surface. Numerous holes were observed in the pericarp. In older pods, the holes were very

evident, however, as some pod walls possessed small, transparent, membrane-covered holes. Apparently, oviposition and larval penetration may occur on growing or immature pods, because new growth of the pericarp has obscured the larval entrance hole.

After the larva has entered the pod, it normally wanders a considerable distance before ascending a funiculus to reach the seed. The seeds are suspended approximately 1.0 to 1.5 mm away from the midrib and the pod wall. Consequently, the larva must climb the stalk or funiculus to reach the seed. After the larva has ascended to the seed, it wedges itself between the distal end of the funiculus and that portion of the seed integument that conceals the distal end of the radicle (Kopooshian and Isely, *1966*; fig. 45, 2D, and C). As a means of gaining purchase, the larva wedges the prothoracic plate against the surface of the funiculus. The pressure on the mandibles apparently facilitates penetration of the seed integument. Once inside, the larva burrows the length of the radicle (fig. 45, 2B) and then abruptly alters its course 180° and burrows along the base of the cotyledons until it reaches an area near the hilum (fig. 45, 2E). When the larva reaches this area it usually is in its second stadium. Immediately, it begins to gnaw a chamber large enough to enable it to rotate 180°. With its dorsum adjacent to the hilum, it begins feeding in semicircular movements until contact is made with the surface of the seed integument. Prior to pupation, the larva again undergoes a 180° rotation, coming to rest with its venter upon the hilum. The larva then partially gnaws through the seed integument in a circular manner, providing an operculum in the integument through which the adult makes its escape.

Most of the time, one complete exuvia and sclerotized portions of earlier exuviae were found tightly packed at one end of the pupal chamber in the seed near the base of the radicle. It is not known why the radicle is left untouched by the developing larva. Perhaps noxious chemicals are concentrated in this area, because it has been reported that this plant causes radical behavior in horses, cattle, and sheep (Kearney and Peebles, *1969*). After pupation, the adult begins chewing around the

operculum, pushes out the operculum, and emerges from the seed. Because the pod walls are thin, the adult easily chews its way out of the pod.

Double and even multiple infestations have been observed in these seeds. These are exceptions, however, because most seeds are infested by a single larva. It is interesting that the second and third larvae to enter a seed always do so through the same burrow initially excavated by the first larva.

In only one of the several hundred seeds that we observed was this behavior different. Then a seed was infested by two larvae. One had entered as described above, but the other had entered the seed near the lens (Kopooshian and Isely, *1966*): fig. 3, *A* and *B*), which is a site opposite the base of the funiculus where the larvae normally enter (fig. 45, *2C*). It is unknown how the larva gained sufficient purchase to penetrate the seed integument. Possibly, two seeds were close enough together to use one as purchase or perhaps the funiculus was bent, thus permitting the seed to rest upon the midrib or the pod wall. The larva could then gain sufficient purchase by forcing the prothoracic plate against any of these.

Cannibalism definitely occurs among larvae of this species. Numerous instances were observed in which nearly mature larvae had devoured earlier instars or earlier instars were feeding upon more mature larvae or a larva had eaten its way into the abdomen (through the tergum) of an adult.

Discussion.—See discussion of *Acanthoscelides aureolus* and *A. baboquivari.*

Acanthoscelides obtectus (Say)

Summary of chaetotaxy: Table 7.

Prothorax (fig. 8).—With nine setae, exclusive of those associated with prothoracic plate (fig. 22, *G*); three small, cuticular lobes near median aspects of segment; three horizontal rows of sclerotized plates (described as minute bristles by Kunhikannan, *1923*) on sternum.

Prothoracic plate (fig. 22, G).—Median arms with one tooth (Kunhikannan, *1923*); posterior arms with five teeth (four to five teeth of Kunhikannan, *1923*, and Riley, *1891*); teeth sub-equal in size; seta 2 (fig. 22, *C*) near median aspects of plate; seta 5 and associated sensory

pore located medially on base of posterior arms; posterior arms broad at base, concealing size of median arms.

Mesothorax and metathorax (fig. 8).—Prodorsum with two setae (*D, d″*). Postdorsum with single seta (*a′*). Mesoepipleuron with primary (*E*) and secondary (*e′*) setae; seta *e′* on metepipleuron. Hypopleuron asetiferous; mesohypopleuron with spiracle and several bordering cuticular projections. Sternum with two setae (*u, R*); many rows of posteriorly directed sclerotized plates.

Legs (fig. 23, G).—Two-segmented (three-segmented, Riley, *1891*); each pair longer than preceding pair (Kunhikannan, *1923*); long pair of decurved setae at distal end of basal segment (Kunhikannan, *1923*); pair of short tactile setae near base of proximal segment; distal end of second segment forming flattened tarsus (lacking tarsal spine shown by Riley, *1892*).

Abdomen (fig. 30).—Prodorsum of segments 1–8 with single seta (*d′*) and associated sensory pore; prodorsum 9 asetiferous; larger pigmented sclerotized tergal plate on segments 8 and 9 (plate on tergite 9 by Kunhikannan, *1923*; anal plate by Riley, *1891*); tergal plate 9 with distinct horizontal suture, giving rise to pro- and postdorsa. Postdorsum of segment 1 with single seta (*A*); postdorsa of segments 2–8 with two setae (*A, a″*); postdorsum 9 with three setae (*A, a′, a″*). Dorsum of segment 10 with seta *g*. Spiracular area of segments 2–8 asetiferous; segment 8 with numerous fleshy cuticular protuberances near spiracle; seta *s′* at posteroventral border of spine on first segment. Epipleuron of segments 1 and 9 with single seta (*E*); single seta (*e′*) on second segment; segments 3–8 with primary (*E*) and secondary (*e′*) setae. Hypopleuron of segments 1–8 with primary seta; hypopleuron 9 with secondary seta; segment 10 lacking hypopleural area of integument. Sternum of segments 1–8 with three setae (*u, v, x*) and many small sclerotized plates; sternites 9 and 10 with seta *v*, without sclerotized plates (contrary to observations of Kunhikannan, *1923*, who reported their presence on these segments). Segment 10 with transverse anal sulcus.

Significant characters.—Each pair of legs longer than preceding pair; median arm of

prothoracic plate with one tooth; sclerotized plate on dorsum of abdominal segments 8 and 9; seta *s'*, *d'*, and *A* on first abdominal segment.

Specimens examined.—26.

Host plants.—Common beans (see Johnson, *1970*).

Biological notes.—Because of its economic importance, considerable work has been done on the life history of *A. obtectus*. There is voluminous literature on the biology of this species (Chittenden, *1898*; Daviault, 1928; Howe and Currie, *1964*; Johnson, *1970*; Kunhikannan, *1923*; Lepesme, *1942*; Riley, *1891*, *1892*; Steffan, *1945*, *1946*; Zacher, *1930*, *1951*).

Discussion.—First instars of *A. obtectus* most closely resemble those of *Algarobius prosopis*. Their prothoracic plates, chaetotaxy, larval and egg-laying behavior are similar (see discussion of *Acanthoscelides baboquivari*).

This species possesses some distinguishing traits that allow separation from other species, that is, the pigmented, sclerotized plate on the dorsum of abdominal segments 8 (previously unrecognized) and 9 and the elongate, curved tactile setae at the distal end of the basal leg segment (Kunhikannan, *1923*; Riley, *1891*, *1892*).

For other distinguishing characters, see discussion of *A. baboquivari*, the above significant characters, and the key.

Acanthoscelides prosopoides (Schaeffer)

Summary of chaetotaxy: Table 8.

Prothorax (fig. 9).—With eight setae, aside from those associated with prothoracic plate (fig. 22, *H*); numerous sclerotized plates on sternum.

Prothoracic plate (fig. 22, H).—Median arms with two teeth, posterior arms with four teeth; seta 2 (fig. 22, *C*) located nearly anteromedially; seta 5 (fig. 22, *C*) decurved; posterior arms not expanded laterally.

Mesothorax and metathorax (fig. 9).—Prodorsum with primary (*D*) and two secondary (*d'*, *d"*) setae. Postdorsum lacking setae. Mesoepipleuron without setae; metepipleuron with single secondary seta (*e'*). Mesohypopleuron with spiracle and two setae (*H*, *h*); metahypopleuron bare. Sternum with pri-

mary (*R*) and secondary (*u*) setae; many large, sclerotized plates.

Legs (fig. 23, H).—Two-segmented; each pair of legs longer than preceding pair; distal tarsus flattened; mesothoracic and metathoracic appendages with pair of sensory pores near proximal end of basal segment; pair of tactile setae at distal end of basal segment.

Abdomen (fig. 31).—Prodorsum of segment 1 with secondary seta (*d"*); segments 2–7 with primary (*D*) and secondary (*d"*) setae; segment 8 with two secondary setae (*d'*, *d"*); segment 9 lacking setae. Postdorsum of segments 1–7 with two secondary setae (*a'*, *a"*); two setae (*A*, *a"*) on segment 8; segment 9 with single primary seta. Dorsum of segment 10 with seta *g*. Spiracular area without setae; spine on segment 1. Epipleuron of segments 1 and 9 with single seta (*E*); second segment with single secondary seta (*e'*); segments 3–8 with two setae (*E*, *e'*). Hypopleuron of segments 1–8 with one seta (*H*); seta *h* on segment 9; segment 10 lacking seta. Sternum of segments 1–7 with three setae (*u*, *v*, *x*); segments 8–10 with single seta (*x*, *x*, and *u*, respectively); numerous sclerotized plates on segments 1–8; segments 9 and 10 lacking sclerotized plates. Segment 10 with transverse anal aperture.

Significant characters.—Each pair of legs longer than preceding pair; median and posterior arms of prothoracic plate with two and four teeth, respectively; seta *D* on prodorsum of abdominal segments 2–7; hypopleuron of abdominal segments 1–8 with seta *H*; absence of *a'* and *a"* on postdorsum of abdominal segment 9; setae *d'* and *d"* on abdominal prodorsum 8; setae *a'* and *a"* on postdorsum of abdominal segments 1–7.

Specimens examined.—12.

Host plants.—*Ziziphus obtusifolia* (Hooker): Arizona. Yavapai Co.: 3 mi N Camp Verde, 3 June 1972. 1.5 mi SW Camp Verde, 3 June 1972, 17 June 1972.

Biological notes.—See Forister and Johnson (*1971*) for information on the life cycle, behavior, ecology, and host plant of this species. The fruit of *Z. obtusifolia* has a bicarpelate ovary with one carpel and ovule much enlarged (Forister and Johnson, *1971*). We observed that a greater percentage of the larvae appeared to prefer the larger ovule, but several larvae also developed within the smaller

ovules, resulting in smaller adults. In several instances, larvae penetrated smaller ovules and appeared to have fed prior to penetrating the septa and entering larger ovules. We also observed that in some fruits the septum separating the two chambers apparently had been penetrated several times by single larvae. Remnants of old exuviae were found within the pupal chamber excavated by the larva. Larvae crawled over the fruit surface following eclosion. This form of behavior is thought to be due to the rather well-developed legs, which may enable the larva to penetrate the surface of the fruit in a manner similar to that described for *Acanthoscelides obtectus* by Kunhikannan (*1923*).

Discussion.—First stage larvae of *A. prosopoides* are the only individuals of the second subgroup (see discussion of *A. baboquivari*) to possess two teeth on each median arm of the prothoracic plate (others possess a single tooth). Other characters are the absence of primary and presence of two secondary setae on the postdorsum of abdominal segments 1–7. This species also lacks the sclerotized abdominal plates of *A. obtectus* and differs from *Algarobius prosopis* in the location of the mesothoracic spiracle (hypopleuron in *Acanthoscelides collusus*; epipleuron in *Algarobius prosopis*).

For other distinguishing features of this species, refer to the above significant characters.

Algarobius prosopis (LeConte)

Summary of chaetotaxy: Table 9.

Prothorax (fig. 10).—With eight setae, exclusive of those associated with prothoracic plate (fig. 22, *I*); several small, cuticular protuberances near posteromedian border; sclerotized plates on sternum.

Prothoracic plate (fig. 22, I).—Median arms with one tooth; posterior arms with seven teeth (six teeth according to Kunhikannan, *1923*); posterolateral aspects of posterior arms extended laterally; seta 2 (fig. 22, *C*) located anteromedially; (not anterolaterally; Kunhikannan, *1923*) seta 5 and associated sensory pore within plate near median border of posterior arms (only one pair of setae along median border of posterior arms, not two pair as shown by Kunhikannan, *1923*).

Mesothorax and metathorax (fig. 10).—Prodorsum bare. Postdorsum of mesothorax with two setae (*A, a″*); metathorax with primary (*A*) and two secondary (*s′, a″*) setae. Mesoepipleuron with two setae (*E, e′*) and spiracle; two or three small, cuticular projections near anterior border of spiracle; metepipleuron with single seta (*e′*). Hypopleuron bare. Sternum with two setae (*u, R*); many sclerotized plates.

Legs (fig. 23, I).—Two-segmented; each pair longer than preceding pair; apical end of distal segment forming flattened tarsus; distal end of basal segment with pair of tactile setae; two sensory pores at base of prothoracic appendage; single sensory pore at base of meso- and metathoracic appendages.

Abdomen (fig. 32).—Prodorsum of segments 1 and 9 bare; segments 2–8 with single seta (*d′*) on prodorsum. Postdorsum of segment 1 with one seta (*a′*); segments 2–8 with two setae (*A, a″*) on postdorsum; postdorsum 9 with primary (*A*) and two secondary (*a′, a″*) setae; seta *a″* twice as long as seta *a′* on segment 9. Dorsum of segment 10 with seta *g*. Spiracular areas asetiferous; spine on segment 1. Epipleuron of segments 1 and 9 with single seta (*E*); secondary seta (*e′*) on segment 2; primary (*E*) and secondary (*e′*) setae on segments 3–8; seta *e′* on segments 3–7 twice as long as seta *e′* on segment 8. Hypopleuron of segments 2–8 with single seta (*H*); segments 1 and 9 with secondary seta; hypopleuron 10 bare. Sternum of segments 1–7 with three setae (*u, v, x*) and sclerotized plates; sternite 8 with two setae (*u, x*); sternites 9 (*v*) and 10 (*x*) with one seta; sclerotized plates absent on segments 8–10. Segment 10 with transverse anal aperture.

Significant characters.—Each pair of legs longer than preceding pair; median arms of prothoracic plate with one tooth, posterior arms with seven teeth; sclerotized, pigmented plates absent on tergites 8 and 9; only seta *a′* on dorsum abdominal segment 1; length of distal setae on basal leg segment greatly reduced.

Specimens examined.—6.

Host plants.—*Prosopis juliflora* (Swartz): Arizona. Yavapai Co.: Verde Valley, summer-fall 1972 (S. Swier).

Biological notes.—See Bridwell (1920, *a, b*),

Forister,[9] Kunhikannan (*1923*, as *Mylabris uniformis*), and Zacher (*1930, 1951, 1952*) for information on life cycle, larval behavior, and host plants. Contrary to reports of Kunhikannan (*1923*), we have observed first instar larvae penetrating pods of *Prosopis juliflora* without utilizing leverage gained by wedging the prothoracic plate against the egg chorion. These larvae crawl over the pod surface following eclosion.

Discussion.—Of the members of the complex mentioned in the discussion of *Acanthoscelides baboquivari, Algarobius prosopis* is the only species with a single tooth on each median arm and seven teeth on each posterior arm. It differs from the closely related *A. obtectus* by characters mentioned in the discussions of *Acanthoscelides obtectus* and *A. baboquivari.* Because of similarities to that species, *A. prosopis* has been placed in a subgroup with *A. obtectus.* We feel that more larvae of the genus *Algarobius* should be studied before our arrangement can be confirmed.

Amblycerus acapulcensis Kingsolver

Summary of chaetotaxy: Table 10.

Prothorax (fig. 11).—With 13 setae, excluding those associated with prothoracic plate (fig. 22, *J*); seta 25 located mesad of seta 16; sclerotized sternal plates obtuse rather than acute.

Prothoracic plate (fig. 22, J).—Median arms with two teeth, median tooth twice as large as lateral tooth; medial border of median arm confluent with same border of posterior arm; posterior arm broad with laterally extended laterodistal border; posterior arm with eight or nine teeth; sensory pore near median base of posterior arm; seta absent on posterior arms; seta 2 located anteromedially, remaining setae near border of anterior arms; two sensory pores located mesad of anterior arms.

Mesothorax and metathorax (fig. 11).—Prodorsum bare. Postdorsum with four setae (*A, a", B, b"*); setae *A, a"* and *B, b', b"* on metathoracic postdorsum. Epipleuron with primary (*E*) and secondary (*e'*) setae. Hypopleuron with single secondary seta (*h*); biforous spiracle on mesohypopleuron. Sternum with

three setae (*u, f, R*) and obtuse sclerotized plates; seta *u* elongate and located mesad of seta *R*.

Legs (fig. 23, J).—Three-segmented; each pair longer than preceding pair; segment 3 terminating in fleshy lobe and opposable crescent shaped, movable sclerotized claw; segment 3 with thin sclerotized plate along anterior surface (may provide rigid surface on which the claw and plate of segment 2 articulate); second and third pairs of appendages possess three tactile setae and two sensory pores near base of fleshy lobe; three setae and one sensory pore near base of fleshy lobe of first appendage; posterior surface of second segment with elongate, decurved, posteriorly directed spine; one spine located laterad and one spine located anterobasally on second segment of legs; sensory pore located medially on lateral side; sclerotized plate along anterior surface of median leg segment provides articular surface for sclerotized plate of basal segment; seta located proximally on anterior surface; basal segment of prothoracic appendage with posteriorly directed seta on caudal surface.

Abdomen (fig. 33).—Prodorsum segments 1–9 with single seta (*d'*); seta *d'* on segments 1–6 with closely associated sensory pore. Postdorsum of segment 1 with three setae (*A, a', a"*); segments 2–6 with four setae (*A, a', a", b'*); segments 7–9 with single primary (*A*) and secondary (*a"*) setae; seta *A* on segment 9 six times longer than seta *A* on segments 7 and 8. Dorsum of segment 10 with two setae (*A, a'*). Spiracles biforous; segment 1 with seta *s'* at base of spine; segments 2–6 with two setae (*s', s"*); segments 7 and 8 possess single seta (*s'*). Epipleuron of segments 1–9 with two setae (*E, e'*). Hypopleuron of segments 1–9 with two setae (*E, e'*). Hypopleuron of segments 1–10 with one seta (*h*). Sternites 1–8 with two setae (*u, v*) and pointed sclerotized plates; single seta (*v*) on sternite 9; sternite 10 bare. Segment 10 with Y-shaped anal sulcus.

Significant characters.—Three-segmented legs, each longer than preceding pair, each possessing internal sclerotized plates; seta *u* mesad of seta *R* on meso- and metathoracic sterna; five pairs of setae between anterior arms of prothoracic plate; setae absent on base of posterior arms of prothoracic plate;

[9] See footnote 7.

setae *A* and *a'* on dorsum of abdominal segment 10.

Specimens examined.—25.

Host plants.—*Caesalpinia cacalaco* Humb. and Bonpl.: Mexico. 6 mi N Los Mochis, Sinaloa, 12 March 1973 (C. D. Johnson).

Biological notes.—Females oviposit at random upon the surface of pods of *Caesalpinia cacalaco.* The eggs may be laid singly or in clusters and may be oviposited in small holes as well as at random over the pod surface. The females appear to attach the eggs by means of the "puddle" technique[10] because of the copious quantities of cement associated with each egg.

Larvae bore from the egg into the pod, but in one instance the larva was prematurely removed from the egg, and its mode of locomotion and general habits were observed. The larva actively crawled for a distance approximately equal to one and one-half times its length and then attached itself to the substrate with the suckerlike tenth abdominal segment. With the abdomen firmly attached to the substrate, the larva then stood upright waving its anterior end about much like a cabbage looper. The larva then resumed its horizontal position. When this larva was placed on the surface of a pod of its host plant, it was able to bore through the side of the pod, without purchase, in about 3 to 5 minutes. This indicates to us that leverage is not necessarily required for penetration of a pod by this species. This behavior may be of importance once the larva has penetrated the pod and entered the chamber containing the ovule. A considerable distance (3 to 9 mm) exists between the ovule and the pod wall. The "looper" behavior would enhance more rapid contact with the seed. Once contact is made with the seed, the larva is capable of boring into the seed without purchase as it did through the pod wall.

Discussion.—This species is readily distinguished from the other species on the basis of host plant preference, behavior, and the significant morphological characters mentioned above. Many of its characters are probably primitive, especially the well-developed thoracic appendages, which possess a termi-

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[10] See footnote 6.

nal, movable claw. Because of this character (Böving, *1930*) in combination with its Y-shaped anal aperture and long primary setae, this species is regarded as being the most primitive of the species involved in this study.

Caryobruchus gleditsiae (Linnaeus)

Summary of chaetotaxy: Table 11.

Prothorax (fig. 12).—With 13 setae, exclusive of those associated with prothoracic plate (fig. 22, *K*); seta 16 arising from sternal lobe; sclerotized plates large, in three horizontal rows.

Prothoracic plate (fig. 22, K).—Median arms absent; broad posterior arms tapering anterolaterally into elongate, narrow anterior arms; posterior arms with 10 rounded teeth; seta 7 isolated in membranous pocket near median aspects of plate; seven pairs of setae associated with plate; setae 1–4 located laterally; setae 5 and 6 located medially.

Mesothorax and metathorax (fig. 12).—Prodorsum greatly reduced. Postdorsum with primary (*A*) and three secondary setae (*a'*, *a"*, *b'*). Epipleuron with primary (*E*) and two secondary setae (*e'*, *e"*); spiracle on mesoepipleuron. Hypopleuron with one seta (*h*). Sternum with three setae (*u, f, R*); seta *u* and *R* restricted to lateral sternal lobes; sclerotized plates on and between sternal lobes.

Legs (fig. 23, K).—With three large segments; curved, sclerotized, immobile claw at apical end of distal segment; three to four tactile setae at distal end of segment 3; prothoracic appendages with sensory pore near anteromedian border of segment 3; segment 2 larger than others, with two tactile setae and two sensory pores; basal segment bare.

Abdomen (fig. 34).—Prodorsum of segments 1–4 (*d'*) and 9 (*d"*) with single seta; seta *d'* on segments 2–8 with closely associated sensory pore; prodorsum of segments 5–8 with two setae (*d', d"*). Postdorsum of segments 1 and 8 with primary (*A*) and two secondary setae (*a', a"*); segment 9 with setae *A* and *a"*; segments 2–7 with four setae (*a", B, b', b"*) on postdorsum. Dorsum of segment 10 with seta *g*. Spiracles biforous; two setae (*s', s"*) on segments 2–8;

segment 1 with three setae (s', s'', s''') near base of spine. Epipleuron of segments 5 and 8 bare; segments 1–4, 6–7, and 9 with primary (E) and secondary (e') setae. Hypopleuron of segments 1–4, 6–7, and 10 with secondary seta only; segment 9 with short primary seta (H); segments 5 and 8 with two setae (H, h). Sternum of segments 1–7 with three setae (u, v, x); sternites 1–7 with mucronate-shaped sclerotized plates; seta u and acute sclerotized plates on sternites 8–10. Segment 10 with Y-shaped anal sulcus.

Significant characters.—Absence of median arms on prothoracic plate; seven pairs of setae associated with prothoracic plate; legs three-segmented; immobile claw at distal end of segment 3; biforous spiracles on thorax and abdomen; mucronate sclerotized plates on abdominal sternites 1–7.

Specimens examined.—20.

Host plants.—*Sabal uresana* Trel.: Mexico. 3 mi W San Carlos Bay, Sonora, 22 December 1972 (C. D. Johnson).

Biological notes.—Because they are very hard, the seeds of the host plant *S. uresana* are sometimes referred to as stone nuts. The seeds are covered by a fragile, spongy tissue that becomes hardened when dry and is easily separated from the seed surface. The females may oviposit on either the covering or the seed.

The oval-shaped egg has a rubbery netlike chorion subtended by a broad band of mucilage. As many as four eggs were oviposited on the same seed, but because we have observed only one adult to emerge from each seed, we assume that cannibalism occurs.

The larva bores into the seed directly from the egg and moves toward the center of the seed where it gnaws a circular chamber. These chambers yielded no evidence of old exuviae, probably indicating that they are consumed by the larva. The chamber is used for pupation, and upon emergence the adult completes the removal of the opercular covering, a task begun by the last instar larva. The adult forces the lid to the outside and escapes through the circular hole.

Discussion.—The host plant (*Sabal uresana*) and significant morphological characters, such as absence of median arms on prothoracic plate, Y-shaped anal aperture, and tarsus, facilitate separation of this species from the others in this study.

Mimosestes amicus (Horn)

Summary of chaetotaxy: Table 12.

Prothorax (fig. 13).—With four setae, exclusive of those associated with the prothoracic plate (fig. 22, *L*); sternum with many large sclerotized plates.

Prothoracic plate (fig. 22, L).—Median arm with two teeth; posterior arm with eight teeth; median tooth on posterior arm elongate with rounded end; medial border of posterior and median arms contiguous; posterior arms broad, short; anterior arms elongate, narrow; seta 5 (fig. 22, *C*) near middle of posterior arm.

Mesothorax and metathorax (fig. 13).—Prodorsum without setae. Postdorsum with primary (A) and two secondary (a', a'') setae; sensory pore closely associated with seta a'. Mesoepipleuron with one primary and one secondary (e') seta; metepipleuron with secondary seta (e') only. Hypopleuron lacking setae; spiracle on mesohypopleuron. Sternum with one seta (R); many large sclerotized plates.

Legs (fig. 23, L).—Two-segmented; subequal in length; flattened tarsus at terminal end of distal segment; pair of tactile setae at apical end of basal segment.

Abdomen (fig. 35).—Prodorsum of segments 1–8 with one seta (d') and associated sensory pore; prodorsum 9 without setae. Postdorsum of segment 1 with seta A; postdorsum of segments 2–8 with two setae (A, a''); distance between setae A and a'' less than half that between same setae on segments 6 and 8; postdorsum 9 with one primary (A) and two secondary setae (a', a''). Dorsum of segment 10 with seta g. Spiracular area lacking setae; three bumps or swellings above spiracle on segments 6–8; spine on segment 1. Epipleuron of segment 1 with single (E) seta; secondary setae only on segments 2–5; primary (E) and secondary (e') setae on segments 6–8, epipleuron 9 bare. Hypopleuron of segments 1–8 with seta h; hypopleura 9 and 10 lacking setae. Sternum of segment 1 without setae; seta x on segments 6–8; seta u on segment 10; two setae (v, x) on segments 2–5 and 9. Segment 10 with transverse anal aperture.

Significant characters.—Legs of subequal length with flattened tarsal complex; enlarged, median tooth on posterior arms of prothoracic plate; median arm of prothoracic plate with two teeth; prothorax with four setae, excluding those of the prothoracic plate; abdominal sternum 1 and abdominal epi- and hypopleuron 9 lacking setae.

Specimens examined.—7.

Host plants.—*Prosopis juliflora* (Swartz): Arizona. Yavapai Co.: Junction of Tuzigoot Natl. Mon. and Hwy. 89, 7 August 1971.

Biological notes.—See Kunhikannan (*1923*) and Forister[11] for information on host plants, developmental time, and behavior. Larvae appear to enter the pod directly from the egg and move within the pod before entering the side of a seed. Larvae always consume considerable quantities of the endosperm before feeding on the cotyledons.

The softer portions of the exuviae are probably consumed because only the heavily sclerotized parts are found within the chamber excavated by the larvae.

Discussion.—See discussion of *Acanthoscelides macrophthalmus*.

Mimosestes protractus (Horn)

Summary of chaetotaxy: Table 13.

Prothorax (fig. 14).—Primary setae absent; five setae present, exclusive of those associated with prothoracic plate; legs absent, replaced by seta 13; four sensory pores near posteromedian border; sternum heavily laden with many large, sclerotized plates.

Prothoracic plate (fig. 22, M).—Median arms with two teeth; posterior arms with six teeth; anterior arms narrow, elongate; posterior arms broad, short, and with laterally extended apical end; setae 2 and 3 (fig. 22, *C*) absent; seta 5 and associated sensory pore near median aspects of posterior arm.

Mesothorax and metathorax (fig. 14).— Primary setae absent. Prodorsum with two setae (*d'*, *d''*). Postdorsum bare. Epipleuron with setae *e'* and *e''*. Mesohypopleuron with two setae (*h'*, *h''*), spiracle, and several small, fleshy lobes anterior to spiracle. Metahypo-

pleuron bare. Sternum with seta *K*; numerous large, sclerotized plates.

Legs.—Absent, replaced by enlarged, decurved spines (setae 13 and *K*, fig. 14).

Abdomen (fig. 36).—Lacking primary setae. Prodorsum of segments 5 and 7 with two setae (*d'*, *d''*); prodorsa 6 and 9 with seta *d'*; prodorsum 9 with oblique row of sclerotized, pointed plates; prodorsum 8 bare. Postdorsum of segment 1 with seta *a''* only; two setae (*a'*, *a''*) on postdorsum of segments 2–8; postdorsum 9 bare. Dorsum of segment 10 with seta *g*. Spiracular areas of segments 3–8 asetiferous, numerous small, sclerotized plates near spiracle; segment 2 with seta *s'*, sclerotized plates lacking; seta *s'* at base of spine on segment 1. Epipleuron of segments 2–8 with single seta; small projections near base of seta on segment 2; epipleura 1 and 9 bare. Hypopleuron of segments 1–7 with one seta; remaining hypopleura (8–10) bare. Sternum of segment 1 with three setae (*u*, *v*, *x*); sternum of segments 2 (*u*, *x*), 3–6 (*u*, *v*), and 9 (*v*, *x*) with two setae; seta *u* on sternite 7; sternites 8 and 10 asetiferous; numerous large, irregularly shaped plates on sternites 1–9; sternite 10 bare. Segment 10 with transverse anal aperture.

Significant characters.—Absence of primary setae and legs; legs replaced by decurved spines; numerous enlarged, posteriorly directed, sclerotized plates on thoracic and abdominal sterna 1–9; three pairs of setae on prothoracic plate.

Specimens examined.—6.

Host plants.—*Prosopis juliflora* (Swartz): Arizona. Yavapai Co.: Verde Valley, summer 1972 (S. Swier).

Biological notes.—See Forister[12] for information concerning percentage infestation, host plant, and oviposition.

Mimosestes protractus infests very immature green pods of *P. juliflora* (personal commun., S. Swier). The absence of thoracic appendages and replacement of them by decurved spines might explain why this species is successful when entering soft pods. The presence of primary setae or longer appendages might impede the movement of a larva through the sappy pulp within a very imma-

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[11] See footnote 7.

[12] See footnote 7.

ture pod. When the female oviposits several eggs on top of each other, the larvae cannot penetrate the pod directly upon hatching, and the presence of the small decurved spines might enhance stability along the pod rib once the larva has vacated the egg (personal commun., S. Swier).

Discussion.—*M. protractus* is most rapidly recognized by the absence of primary setae and segmented walking appendages. These traits ally it to the group that includes *Zabrotes subfasciatus, Stator limbatus, S. pruininus,* and *S. pygidialis.*

Due to the reduction in size of the prothoracic plate, the number of setae (three pairs) associated with the plate, and location of spiracle on hypopleuron, *M. protractus* is considered to be most closely related to *Z. subfasciatus.* Because these traits are considered to be the most derived, we consider these species to be the most advanced of those involved in this study.

There are, however, numerous differences between the two species. Probably the most recognizable is the degree of development of the prothoracic plate. The plate of *Zabrotes subfasciatus* (fig. 22, *T*) is represented only by a pair of toothlike sclerotized projections, which represents what we consider to be a derived trait, whereas, anterior, median, and posterior arms are present on the plate of *M. protractus.* In addition, *M. protractus* possesses five pairs of setae on the prothorax (15 pairs in *Z. subfasciatus*) and numerous enlarged, sclerotized plates on all sternites (absent in *Z. subfasciatus*) and is restricted to the host plant *Prosopis juliflora.*

Mimosestes sallaei (Sharp)

Summary of chaetotaxy: Table 14.

Prothorax (fig. 15).—With nine setae, exclusive of five pairs associated with prothoracic plate (fig. 22 *N*); two distinct rows of small, sclerotized plates near upper anterior portion of segment, near distal end of anterior arms of prothoracic plate; sternum with few sclerotized plates.

Prothoracic plate (fig. 22, N).—See Kunhikannan (*1923, plate III, figs. 6 and 8*); median arm with two teeth, one large and one small; posterior arm with numerous teeth,

medial tooth elongate and pointed (noted by Kunhikannan, *1923*), remaining teeth nearly equal in size; posterior arm expanded laterally; seta 2 (fig. 22, *C*) nearly anteromedial; sensory pore or pit between setae 1 and 2.

Mesothorax and metathorax (fig. 15).—Prodorsum without setae. Postdorsum with primary (*A*) and two secondary setae (*a', a"*); setae *A* and *a"* close together and located near ventral aspects of postdorsum. Mesoepipleuron with two setae (*E, e'*); metepipleuron with single secondary seta (*e'*). Hypopleuron lacking setae; spiracle on mesohypopleuron. Sternum with two setae (*R, u*); moderate number of small sclerotized plates in one or two rows.

Legs (fig. 23, M).—Two-segmented; each pair longer than preceding pair; tarsus flattened; pair of tactile setae at distal and proximal ends of basal segment; small sensory pore located anteromedially on first and second pairs of legs.

Abdomen (fig. 37).—Prodorsum of segments 1–8 with one seta (*d'*); segment 9 lacking setae. Postdorsum of segment 1 with seta *A*; postdorsa of segments 2–8 with two setae (*A, a"*); postdorsum 9 with setae *A, a',* and *a".* Dorsum of segment 10 with seta *g.* Spiracular area of segment 1 with seta *s'* and spine; segments 2–4 with small conical-shaped bumps located anterodorsal to spiracle; remaining segments 5–8 lacking setae or bumps. Epipleuron of segments 1 and 9 with one seta (*E*); segments 2–4 with secondary setae only; segments 5–8 with primary (*E*) and secondary (*e'*) setae. Hypopleuron of segments 1–9 with single secondary seta only; segment 10 lacking setae. Sternum of segments 1–7 with three setae (*u, v, x*) and numerous sclerotized plates; sternum 8 with two setae (*v, x*) and few sclerotized plates; seta *v* on segments 9 and 10; sclerotized plates scarce on segment 9. Segment 10 with transverse anal aperture.

Significant characters.—Each pair of legs longer than preceding pair; median arm of prothoracic plate with two teeth; seta *D* absent on abdominal prodorsa; hypopleuron of abdominal segments 1–9 with secondary setae only; setae *a'* and *a"* on ninth abdominal postdorsum; median tooth on posterior arm of prothoracic plate elongate and apically pointed; seta *A* on first abdominal postdor-

sum; seta s' on first abdominal spiracular area.

Specimens examined.—46

Host plants.—*Acacia farnesiana* (Linnaeus): Mexico, 8 mi S Atenquique, Jalisco, 3 January 1973 (C. D. Johnson).

Biological notes.—For host plant information, see Zacher (*1952*). Larvae used in this study were obtained from the seeds of *A. farnesiana.* Information is also available on the bionomics (Cushman, *1911*; Hinckley, *1960, 1961*), ovipositional behavior (Hinckley, *1960, 1961*), egg characteristics (Cushman, *1911*; Hinckley, *1960*; Kunhikannan, *1923*), and parasites of eggs, larvae, and adults (Cushman, *1911*; Hinckley, *1960, 1961*).

We have observed that larvae may leave the egg by way of the anterodorsal end and crawl over the pod surface. These larvae move to the sulcus of the seam uniting the two halves of the pod where they are able to acquire sufficient leverage to penetrate the pod coat.

Oviposition appears to occur at random over the pod surface and in old exit holes and pupal chambers. Generally, however, females seem to prefer the slight depression along the side of the ridge of the pod seam for oviposition. Perhaps this behavior is a mechanism to ensure larval survival because Hinckley (*1960*) reported some eggs are not always firmly attached. Therefore, if the eggs are laid next to the seam, the newly hatched larva need only crawl a short distance (less than 2 mm) to penetrate the pod.

Discussion.—*Mimosestes sallaei* is one in a group of three rather distantly related species. These species are thought to be related because they all possess the following characters: Two teeth on each median arm and an elongate, pointed, median tooth subtended by seven or eight smaller teeth on each posterior arm; similar chaetotaxy. For additional discussion see that of *Acanthoscelides macrophthalmus.*

Neltumius arizonensis (Schaeffer)

Summary of chaetotaxy: Table 15.

Prothorax (fig. 16).—With seven setae, exclusive of those associated with prothoracic plate (fig. 22, *O*); sternum with two or three irregular rows of sclerotized plates.

Prothoracic plate (fig. 22, O).—Median arms with three or four teeth; posterior arms with five or six teeth; posterior arms short and broad, anterior arms elongate and narrow with enlarged cephalic end; setae 2, 3, and 4 (fig. 22, *C*) not bordering plate, located more medially; seta 5 near median aspects of base of posterior arm, associated sensory pore near median border of posterior arm.

Mesothorax and metathorax (fig. 16).—Prodorsum lacking setae. Postdorsum with primary (*A*) and secondary (*a', a"*) setae. Mesoepipleuron with two setae (*E, e'*); metepipleuron with seta *e'*. Hypopleuron without setae; spiracle on mesohypopleuron. Sternum with one seta (*R*); three or four irregular rows of sclerotized plates.

Legs (fig. 23, N).—Two-segmented; subequal in length; apical end of distal segment with rounded tarsus; pair of tactile setae located distally on basal segment; large sensory pore at base of proximal segment.

Abdomen (fig. 38).—Prodorsum of segment 1 with primary seta only; segments 2–6 and 8 with one seta (*d'*); sensory pore associated with seta *d'* on segments 2–6; prodorsum 7 with two secondary setae (*d', d"*); prodorsum 9 without setae. Postdorsum of segments 1 and 7 with setae *a'* and *a"*, respectively; segment 2 with one seta (*A*); segments 3–6 and 8 with setae *A* and *a"*; setae *a'* and *A* on segment 9, distance between setae exceeds half the length of seta *A*. Dorsum of segment 10 with seta *g*. Spiracular areas without setae; spine on segment 1. Epipleuron of segments 1 and 9 with one seta (*E*); segments 2–4 with secondary seta only; two setae (*E, e'*) on segments 5–8. Hypopleuron of segments 1–9 with secondary seta; hypopleuron 10 bare. Sternum of segments 2–8 with three setae (*u, v, x*); setae *u* and *v* on segment 1; seta *v* on segment 9; segment 10 without setae or sclerotized plates; segments 1–9 with one to several irregular rows of sclerotized plates. Segment 10 with transverse anal aperture.

Significant characters.—Legs of subequal length, with rounded tarsus; primary seta *A* on postdorsum of abdominal segment 6; meso- and metahyposternum bare; seta *h* on abdominal segment 9; median arm of prothoracic plate with at least three teeth.

Specimens examined.—15.

Host plants.—Prosopis juliflora (Swartz): Arizona. Yavapai Co.: Verde Valley, summer-fall 1972 (S. Swier).

Biological notes.—See Forister (*1970*) for information on egg characteristics, developmental period, and generations per year; Kingsolver (*1964*) for host plant information; and Kunhikannan (*1923*) for egg characteristics and larval behavior and characters information.

Discussion.—N. arizonensis represents a species distinct from others involved in this study. The similarities shared with *Sennius morosus* are mentioned in the discussion of that species. For other distinguishing differences, see biological notes and significant characters mentioned above.

Sennius morosus (Sharp)

Summary of chaetotaxy: Table 16.

Prothorax (fig. 17).—With 11 setae, exclusive of those associated with prothoracic plate (fig. 22, *P*); numerous enlarged sclerotized plates on sternal lobes between appendages.

Prothoracic plate (fig. 22, P).—Median arms with two teeth of variable sizes; posterior arms with six teeth (five contiguous and one lateral); seta 4 (fig. 22, *C*) missing; seta 5 within plate of posterior arm, associated sensory pore on median border of posterior arm; seta 2 located medially; distal end of posterior arms extended laterally; anterior arms tapering from base to apex.

Mesothorax and metathorax (fig. 17).—Prodorsum lacking setae. Postdorsum with three setae (*A, a', a''*); setae *A* and *a''* nearly contiguous, near tergo-pleural border; seta *a'* and associated sensory pore located dorsally. Epipleuron with two setae (*E, e'*). Hypopleuron bare; spiracle on mesohypopleuron. Mesosternum with two setae (*u, R*) and numerous sclerotized plates on sternal lobes; few plates between and behind lobes; metasternum with four setae (*u, v, x, R*) and sclerotized plates on sternal lobes.

Legs (fig. 23, O).—Two-segmented; subequal in length; apical end of distal segment forming rounded tarsus; three tactile setae on basal segment of meso- and metathoracic appendages; two setae on basal segment of prothoracic leg.

Abdomen (fig. 39).—Prodorsum of segment 1 bare; prodorsa of segments 2–9 with single seta (*d'*); seta *d'* on segments 2–8 with closely associated sensory pore. Postdorsum of segments 1–5 and 7–9 with two setae (*A, a''*); postdorsum 6 bare. Dorsum of segment 10 with seta *g*. Spiracular areas of segments 2–8 asetiferous; segments 2–5 with several small, fleshy projections above spiracle; segment 1 with seta (*s'*) at base of spine. Epipleuron of segments 1 and 9 with one seta (*E*); secondary seta (*e'*) on segments 2–5; remaining epipleura (6–8) with two setae (*E, e'*). Hypopleuron of segments 1–9 with secondary seta only; hypopleuron 10 bare; sterna asetiferous; numerous large sclerotized plates on segments 1–8, plates reduced in size on sternites 9 and 10. Segment 10 with transverse anal aperture.

Significant characters.—Legs of subequal length and a rounded tarsus; three pairs of setae between anterior arms of prothoracic plate; abdominal sterna lacking setae *u, v*, or *x*; hyposternal setae absent on meso- and metathorax.

Specimens examined.—32.

Host plants.—Cassia bauhinioides Gray: Arizona. Yavapai Co.: 1 mi S junction of Beaver Creek—Montezuma Well roads, 4 September 1971, 17 June 1972.

Biological notes.—Detailed information concerning the life history, habits, and host plant records of this species was presented by Center and Johnson (*1973*) and Johnson and Kingsolver (*1973*). We have observed that larval entry occurs consistently between the septa and the adjacent seed surface. Apparently the most effective leverage necessary for seed penetration is acquired at that point. Instances of two larvae infesting the same seed were observed, indicating that cannibalism does exist because only a single adult emerges from a seed or seeds. Most seeds are infested by a single larva, and, after penetration of the seed test, the larva appears to feed on the endosperm for at least one and maybe two stadia before entering the cotyledons.

Larvae do not appear to consume the old integument because two or three nearly complete exuviae were found tightly packed at one end of the pupal chamber.

Discussion.—Sennius morosus is quite different from any other species involved in this

study because only four pairs of setae are associated with the prothoracic plate (a character shared by the genus *Stator*, see discussion of *Stator limbatus*) and the abdominal sternites are devoid of setae. These are considered to be an advanced trait; consequently, *S. morosus* is placed near that complex mentioned in the discussion of *Mimosestes protractus*. *S. morosus* does possess primary setae and segmented walking appendages that distinguish it from the more advanced group of *Stator, Mimosestes protractus* and *Zabrotes subfasciatus*.

The larvae of *S. morosus* are most similar to those of *Neltumius arizonensis*. The legs of *S. morosus* are subequal in length and possess a rounded tarsus. Except for the sternites, the chaetotaxy is identical on the meso- and metathorax. However, numerous differences do exist between these two species, that is, setae on the thoracic sterna of *S. morosus* (absent on *N. arizonensis*), five pairs of setae associated with prothoracic plate of *N. arizonensis*, and setae on abdominal sternites of *N. arizonensis*. Because of these differences, we consider them to be distantly related species.

Stator limbatus (Horn)

Summary of chaetotaxy: Table 17.

Prothorax (fig. 18).—Lacking primary setae; nine setae present, exclusive of those associated with prothoracic plate (fig. 22, Q); legs absent, replaced by seta 23; many small, sclerotized plates across sternum.

Prothoracic plate (fig. 22, Q).—(Kunhikannan, *1923*) median arms with two teeth; posterior arms with five teeth, median tooth narrow and elongate; distal end of posterior arms terminating in lateral, quadrate projection; four pairs of secondary setae; seta 4 (fig. 22, C) absent; seta 5 and associated sensory pore located mesad of medial border of posterior arms; width of posterior arm base greatly narrowed.

Mesothorax and metathorax (fig. 18).—Primary setae absent. Prodorsum of mesothorax bare; metathoracic prodorsum with three setae (*d', d", d'''*); seta *d'* with associated sensory pore distant from other two setae. Postdorsum of mesothorax with three setae (*a', a", b'*); seta *a'* with associated sensory

pore, near middle of tergum; setae *a"* and *b'* near pleurotergal border; metathoracic postdorsum with single seta (*a'*) and associated sensory pore. Mesoepipleuron with two setae (*e', e"*); spiracle in anteroventral area of subsegment; metepipleuron with single seta (*e'*). Hypopleuron bare. Legs replaced by seta *K*; small, sclerotized plates.

Legs.—Absent (Kunhikannan, *1923*), replaced by setae 23 (on prothorax) and *K* (on meso- and metathorax) (fig. 18).

Abdomen (fig. 40).—Primary setae absent. Prodorsa bare. Postdorsum of segments 1 and 9 with two setae (*a', a"*); three setae (*a', a", b'*) on postdorsum of segments 2–8; seta *a'* on segments 1–7, with closely associated sensory pore; setae *a"* and *b'* closely associated but distant from seta *a'*. Dorsum of segment 10 with seta *g*. Spiracular area of segments 2–8 without setae; small, sclerotized projections posterior and ventral to spiracle on segments 2–8; seta *s'* at base of spine on segment 1. Epipleuron of segments 1–7 and 9, with one seta (*e'*); epipleuron 8 with two setae (*e', e"*). Hypopleuron of all segments (1 to 10) with seta *h*. Sternum of segments 1–9 with single seta (*v*); sensory pore evident anterolaterally of seta *v* on segments 1–7; few small sclerotized plates on segments 1–9; sternite 10 bare. Segment 10 with transverse anal aperture.

Significant characters.—Absence of primary setae; legs replaced by short, acute setae; median arms of prothoracic plate with two pairs of teeth, posterior arms with five pairs; posterior arms terminating in lateral, quadrate projection; three pairs of setae between anterior arms; single seta on abdominal sterna.

Specimens examined.—61.

Host plants.—*Acacia millefolia* Wats.: Arizona. Pima Co.: Box Canyon, Santa Rita Mts., 7 October 1972 (C. D. Johnson).

Biological notes.—For information concerning life history, ecology, oviposition, and host plants of this species, consult Forister,[13] Johnson (*1967*), Kunhikannan (*1923*), Zacher (*1930, 1951*), and Johnson and Kingsolver (*In press*).

Eggs may be laid singly or in clusters with a narrow band of mucilage around each. In

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[13] See footnote 7.

many instances, the glue served to connect numerous eggs together. The egg is similar to that of *Stator pruininus* (fig. 45, 3), but differs from that of *S. pygidialis* in that it lacks the prominent anterior middorsal point characteristic of that species (fig. 45, 4). We found complete exuviae in pupal chambers, indicating that exuviae are not partially or completely consumed.

Discussion.—The adults of *Stator limbatus*, *S. pruininus*, and *S. pygidialis* are very closely related in their behavior and morphology; consequently, they form a very distinct genus (Johnson and Kingsolver, *in press*). The larvae also form a distinct group on the basis of morphology and behavior.

These three species are readily separated from *Mimosestes protractus* and *Zabrotes subfasciatus* because they have an elongate, pointed, median tooth on the posterior arm of the prothoracic plate (see figs. 22, *Q*, *R*, and *S*). In addition, the mesothoracic spiracle is on the epipleuron (hypopleuron in *M. protractus* and *Z. subfasciatus*), and four pairs of setae are associated with the prothoracic plate (three pairs in *M. protractus* and *Z. subfasciatus*).

The five teeth on each posterior arm of the prothoracic plate of *S. limbatus* serve as a useful criterion for species separation. Only three teeth appear on each posterior arm of the plate of *S. pruininus* and *S. pygidialis*. Also, *S. limbatus* lack seta *d* on the prodorsum, a character typical of the other two species.

Stator pruininus (Horn)

Summary of chaetotaxy: Table 18.

Prothorax (fig. 19).—Primary setae absent; with nine pairs of setae, exclusive of four pairs associated with prothoracic plate (fig. 22, *R*); sternum with numerous small, cuticular lobes surrounding seta 24; legs absent, replaced by setae (24).

Prothoracic plate (fig. 22, R).—Median arms with one or two teeth; posterior arms with three teeth; one elongate, pointed median tooth, two small, rounded teeth of subequal size (not shown by Kunhikannan, *1923*); laterodistal aspects of posterior arms extended laterally; anterior arms, extended anterolaterally, possessing subparallel sides; three

pairs of setae between anterior arms; seta 3 (fig. 22, *C*) missing; seta 2 not located anteromedially, as shown by Kunhikannan (*1923*); seta 5 and associated sensory pore along medial border of posterior arm.

Mesothorax and metathorax (fig. 19).—Primary setae absent. Prodorsum bare. Postdorsum with three setae (*a'*, *a''*, *b'*). Epipleuron of mesothorax with two setae (*e'*, *e''*); sensory pore and spiracle; metepipleuron with single seta (*e'*). Hypopleuron with one seta (*h*). Sternum with numerous small, cuticular lobes surrounding seta *K*; only seta *K* present.

Legs.—Absent, replaced by setae 24 and *K* (fig. 19); sternal projections, shown by Kunhikannan (*1923*), not evident.

Abdomen (fig. 41).—Lacking primary setae. Prodorsum of segments 1–7 with seta *d'*; prodorsum bare on segment 8, absent on segments 9 and 10. Postdorsum of segment 1 with single seta (*a''*); postdorsa 2–7 with setae *a''* and *b'*; postdorsum 8 and dorsum of segment 9 with three setae (*a'*, *a''*, *b'*). Dorsum of segment 10 with seta *g*. Spiracular area of segments 2–8 asetiferous; segment 1 with seta *s'* at base of spine. Epipleuron of segments 1–5 with seta *e'*; two setae (*e'*, *e''*) appear on epipleuron of segments 6–8, epipleuron 9 bare. Hypopleuron of segments 1–10 with single seta (*h*). Setae *u* and *v* on sternites 1–7; one sclerotized plate and several small, cuticular projections on segments 1–5; two to four large, pigmented, sclerotized projections on sternites 7 and 8; small, cuticular projections on segments 6–8 and sternites 9 and 10 bare. Segment 10 with transverse anal aperture.

Significant characters.—Absence of primary setae; legs replaced by short, acute setae; large, pigmented, sclerotized projections on abdominal sternites 7 and 8; posterior arms with three teeth; median tooth elongate, pointed; two teeth on right median arm, left median arm with one tooth.

Specimens examined.—48; reared from seeds of *Mimosa grahami* Gray: Arizona. Cochise Co.: Cochise Stronghold, 14 October 1973 (C. D. Johnson).

Biological notes.—A wide range of plants serve as host for this species (Bridwell, *1918*; Johnson, *1967*; Zacher, *1952*). Several eggs may be laid upon a single seed (Bridwell, *1918*;

Johnson, *1967*), resulting in smaller adults. The egg (fig. 45, 3) (described by Bridwell, *1918*, and Kunhikannan, *1923*), which differs morphologically from that of the closely related species *Stator pygidialis* (fig. 45, 4), possesses a broad band of mucilage, which increases greatly in width toward and at the anterior end. Larval behavior during and subsequent to eclosion has also been discussed by these authors. Forister[14] reported upon its parasites, whereas Bridwell (*1918*) discussed adult mating behavior.

The functional significance of the large, sclerotized, pigmented projections on sternites 7 and 8 appears to be that of gaining added thrust when larvae tunnel through the cotyledons.

Discussion.—*Stator pruininus* shares a number of morphological similarities with *S. limbatus* but more closely resembles *S. pygidialis*. Setae *u* and *v* (on meso- and metathoracic sterna of *S. pygidialis*) are absent on meso- and metathoracic sterna of *S. pruininus*. *S. pruininus* has setae 24 and *K* on its thoracic sternites and two to four large sclerotized projections on abdominal sternites 7 and 8, but these are absent on *S. pygidialis*. *S. pruininus* also lacks setae 15 and 17, which are on the prothoracic sternite of *S. pygidialis*.

The distinguishing feature of the first instar of *S. pruininus* is the presence of two to four large, pointed, pigmented, posteriorly directed, sclerotized plates on the sternum of abdominal segments 7 and 8.

Stator pygidialis (Schaeffer)

Summary of chaetotaxy: Table 19.

Prothorax (fig. 20).—Primary setae absent; with 10 pairs of setae, exclusive of 4 pairs associated with prothoracic plate (fig. 22, *S*); several small, cuticular lobes on sternum; jointed appendages replaced by lateral lobes, which possess distally a sensory pore and two setae.

Prothoracic plate (fig. 22, S).—Median arm with two teeth of subequal size; posterior arm with three teeth; medial tooth elongate and pointed, subtended by two smaller teeth of equal size; laterodistal aspects of posterior arms extended laterally into quadrate-shaped

projections; anterior arms extended anterolaterally; three pairs of setae between anterior arms; seta 4 (fig. 22, *C*) absent; setae 2 and 3 located medially, not arranged along medial border of anterior arm; sensory pore located anterolaterally of seta 2; seta 5 and associated sensory pore located mesad of median border of posterior arm.

Mesothorax and metathorax (fig. 20).—lacking primary setae. Prodorsum bare. Postdorsum with three setae (*a'*, *a"*, *b'*); seta *a'* with closely associated sensory pore. Mesoepipleuron with two setae (*e'*, *e"*), sensory pore located anterodorsally to spiracle; metepipleuron with one seta (*e'*) and sensory pore located anterodorsally. Hypopleuron bare. Sternum with two setae (*u*, *v*) and several small, cuticular lumps; legs replaced by lateral, fleshy lobes.

Legs.—Absent, replaced by rudiments in the form of lateral lobes (Snodgrass, *1935*). Each lobe with two distal tactile setae; single sensory pore on mesothoracic lobe; metathoracic lobe with two sensory pores.

Abdomen (fig. 42).—Primary setae absent. Prodorsum of segments 1–7 with seta (*d'*) and associated sensory pore; prodorsum 8 bare; plicae absent on dorsum of segment 9. Postdorsum of segment 1 with one seta (*a"*); postdorsa 2–7 with two ventral setae (*a"*, *b'*); postdorsa 8 and 9 with three setae (*a'*, *a"*, *b'*). Dorsum of segment 10 with seta *g*. Spiracular area of segments 2–8 asetiferous; seta *s'* at base of spine and dorsad of spiracle on first segment. Epipleuron of segment 1 with seta (*e'*) and several posteriorly located, pointed, cuticular projections; epipleura 2–5 with single seta (*e'*); setae *e'* and *e"* on epipleuron of segments 6–8; epipleuron 9 bare. Hypopleura 1–10 with seta *h*. Sternites 1–7 with two setae (*u*, *v*) and numerous cuticular lobes; only seta *v* on sternites 8 and 9; single horizontal row of cuticular lobes between setal pair (*v*) on sternum 8; sternite 10 bare. Segment 10 with transverse anal aperture.

Significant characters.—Primary setae and legs absent; legs replaced by lateral lobes; median arm of prothoracic plate with two teeth of equal size; posterior arm with three teeth, median tooth elongate and pointed; two lateral teeth short, of subequal size; rows of

pointed, cuticular projections along caudal aspects of first epipleuron.

Specimens examined.—7.

Host plants.—*Calliandra humilis* Benth.: Arizona. Coconino Co.: Base, south slope, Mt. Elden, Flagstaff, fall 1973 (C. D. Johnson).

Biological notes.—The larva penetrates the seed directly from the egg. Egg morphology differs from that of *Stator limbatus* and *S. pruininus* (fig. 45, 3) by possessing anteriorly a very distinct middorsal point (fig. 45, 4). The egg is oval, possessing a wide anterior end and is bound to the seed surface by a broad band of mucilage. The mucilage probably provides a means by which the larva may gain sufficient purchase to penetrate the egg chorion and seed integument.

Discussion.—The two teeth on each median arm of the prothoracic plate of *S. pygidialis* and the paired lateral lobe appendages on the thoracic sterna serve as criteria for separating this species from other species within the genus. The anteriorly located, middorsal point on the surface of the egg of *S. pygidialis* (fig. 45, 4) is also a very useful criterion for separating the species within this genus. The egg surface is convex in *S. limbatus* and *S. pruininus* (fig. 45, 3).

A more thorough discussion of the genus is presented in the discussion of *S. limbatus*. For a discussion of the species within the group lacking primary setae and legs, see the discussion of *Mimosestes protractus*.

Zabrotes subfasciatus (Boheman)

Summary of chaetotaxy: Table 20.

Prothorax (fig. 21).—Primary setae absent; 15 pairs of secondary setae present, exclusive of those associated with prothoracic plate; prothoracic appendage replaced by seta *24*; sclerotized plates absent.

Prothoracic plate (fig. 22, T).—Kunhikannan (*1923*), Steffan (*1945*), and Zacher (*1930*) mentioned the reduction in development of the prothoracic plate. The illustration of Zacher is most accurate. In addition to the externally projecting teeth of the posterior arms, he also showed the subintegumental remnants of the median and anterior arms. Differences are reported in the numbers of projecting teeth. Our observations that two

teeth are present agree with those of Kunhikannan and Steffan. Zacher reported two to three projecting teeth per prothoracic arm.

Mesothorax and metathorax (fig. 21).—Without primary setae. Prodorsum bare. Postdorsum with two setae (*a'*, *a"*). Epipleuron with single seta (*e'*). Hypopleuron with one seta (*h*); spiracle on mesohypopleuron. Sternum without sclerotized plates; legs replaced by seta *K*.

Legs.—Absent (Kunhikannan, *1923*; Steffan, *1945*; Zacher, *1930*); replaced by setae *24* and *K* (fig. 21).

Abdomen (fig. 43).—Primary setae absent. Prodorsum of segment 1 with two setae (*d'*, *d"*); segments 2–7 with single seta (*d'*); prodorsa 8 and 9 bare. Postdorsum of segment 1 with single seta (*a'*); postdorsa of segments 2–9 with setae *a'* and *a"*. Dorsum of segment 10 with seta *g*. Spiracular area of segments 2–8 bare; segment 1 with seta *s'* at base of spine, both located dorsad to spiracle. (Seta *s'* is always on abdominal segment 1, contrary to reports by Steffan (*1945*) that seta *s'* is sometimes present.) Epipleuron of segments 1–8 with two setae (*e'*, *e"*); segment 9 with single seta (*e'*). Hypopleuron of segments 1–9 with one seta (*h*); hypopleuron 10 bare. Sternum lacking sclerotized plates; setae *u* and *v* on segments 1–8; one seta present on sternites 9 (*v*) and 10 (*u*). Segment 10 with transverse anal aperture.

Significant characters.—Absence of primary setae and legs, the latter replaced by small, pointed setae; reduction in development of the prothoracic plate; three pairs of setae between arms of prothoracic plate; numerous (15) setae on prothorax; posteriorly curved seta at base of spine on spiracular area of first abdominal segment.

Specimens examined.—20.

Host plants.—Common beans.

Biological notes.—Due to its economic significance, much has been written about this organism. Howe and Currie (*1964*), Steffan (*1945*), and Zacher (*1930*) presented detailed accounts of the life history and factors affecting oviposition, developmental rate, and mortality. Information is also available concerning larval morphology, behavior, and food plants (Kunhikannan, *1923;* Steffan, *1945;*

Zacher, *1930, 1951, 1952*). Zacher (*1951, 1952*) listed feeding habits and preferences of the adults and, in addition, listed 13 plants that may serve as potential hosts.

Discussion.—Z. subfasciatus, due to its habit of infesting stored legumes, is a species of major economic importance and cosmopoli-

tan distribution. The first instar larva is most easily recognized by the reduction in development of its prothoracic plate (fig. 22, *T*). For other distinguishing differences, see discussion of *Mimosestes protractus*. This species was treated under the name *Z. pectoralis* by Kunhikannan (*1923*).

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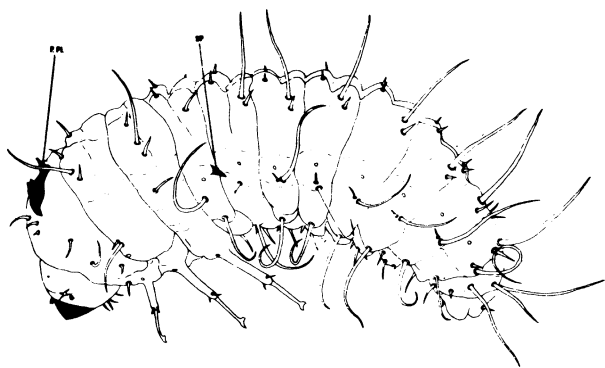
FIGURE 1.—Generalized first instar larva showing primary (long) and secondary (short) setae. p.pl.: prothoracic plate; sp.: first abdominal spine. Scale line = 1.0 mm.
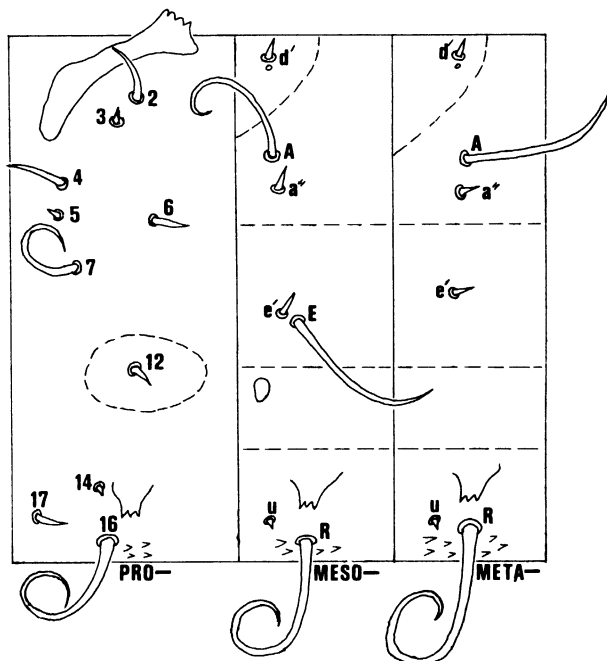
FIGURE 2.—Thoracic setal map: *Acanthoscelides aureolus*.
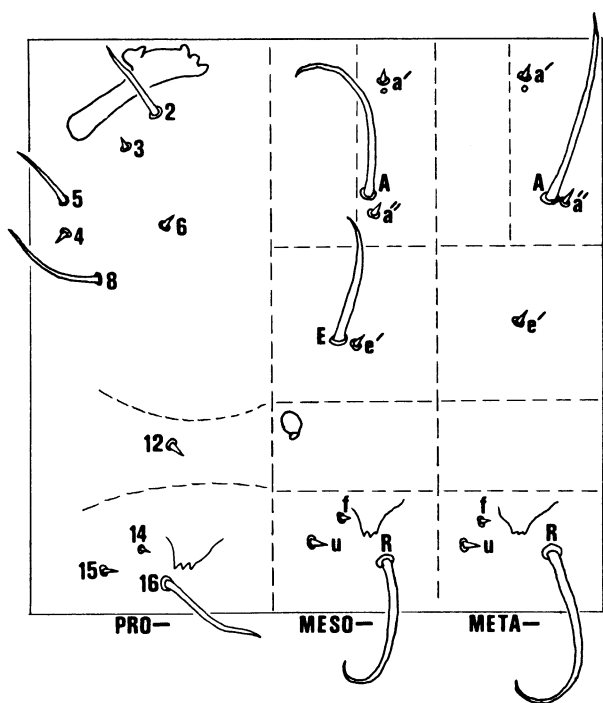
FIGURE 3.—Thoracic setal map: *Acanthoscelides baboquivari*.
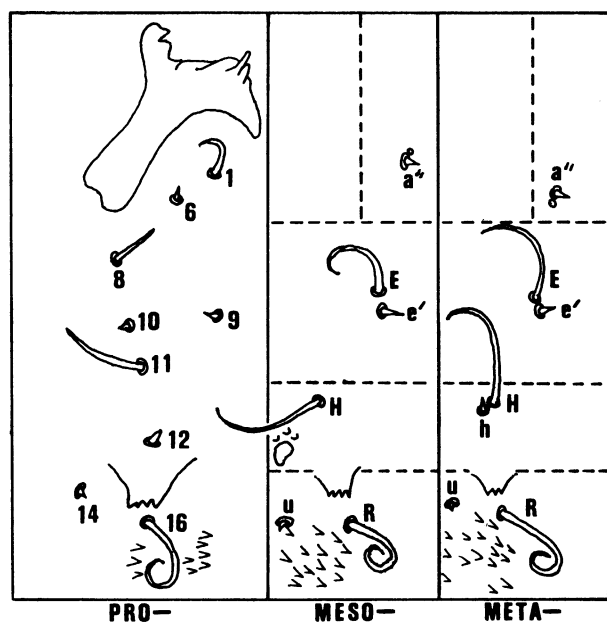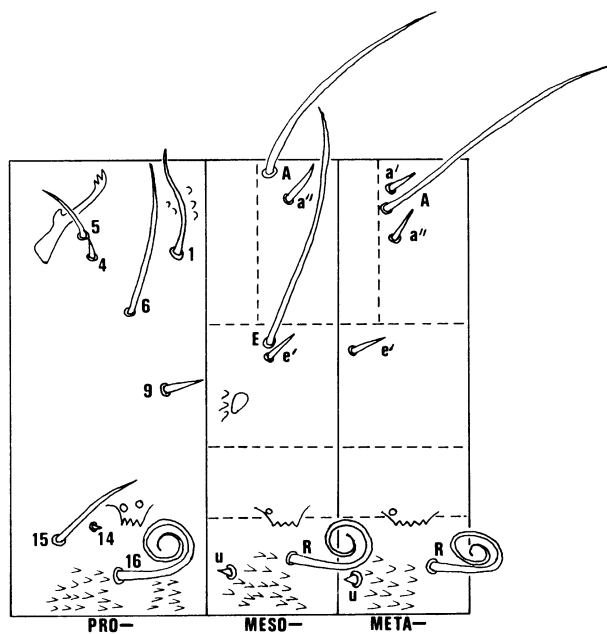

FIGURE 4.—Thoracic setal map: *Acanthoscelides chiricahuae*.
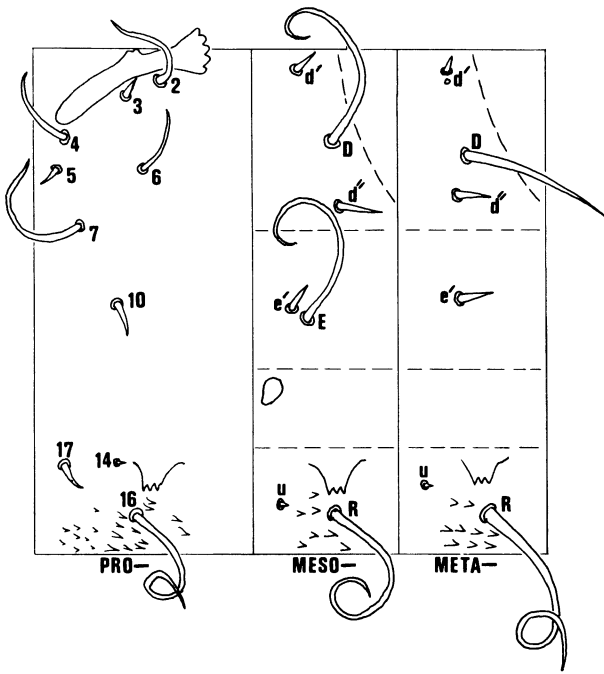
FIGURE 5.—Thoracic setal map: *Acanthoscelides collusus.*
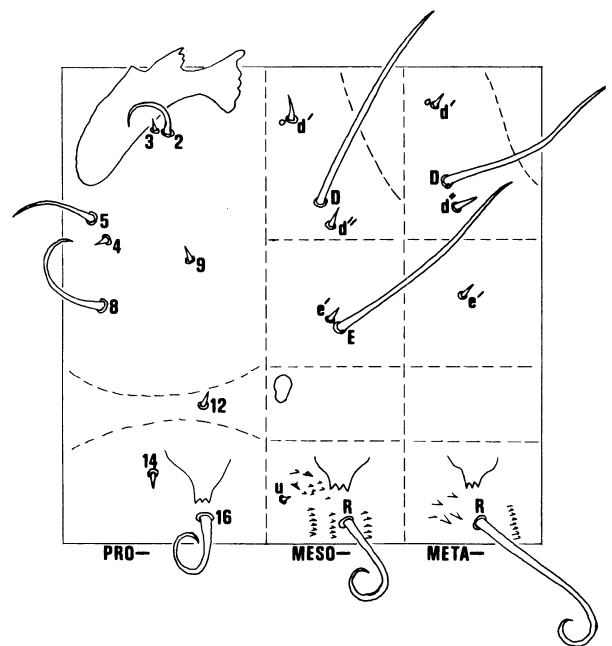
FIGURE 6.—Thoracic setal map: *Acanthoscelides macrophthalmus.*
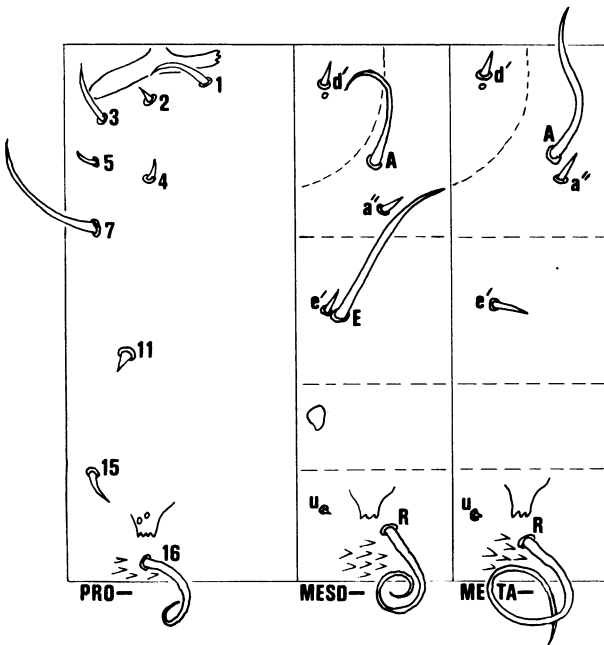
FIGURE 7.—Thoracic setal map: *Acanthoscelides mixtus.*
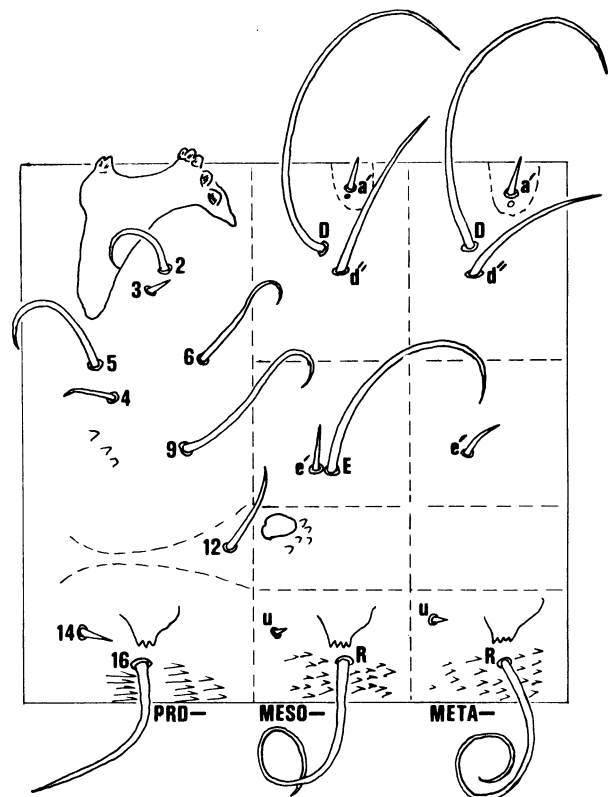
FIGURE 8.—Thoracic setal map: *Acanthoscelides obtectus.*
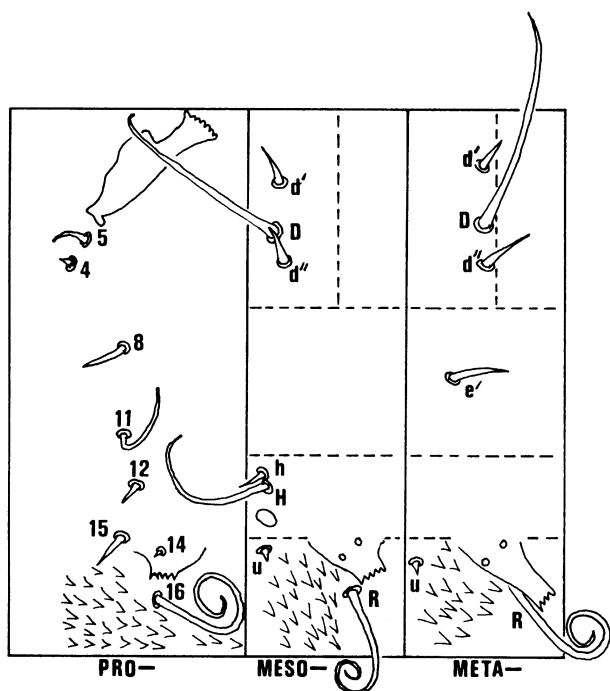
FIGURE 9.—Thoracic setal map: *Acanthoscelides prosopoides.*

FIGURE 10.—Thoracic setal map: *Algarobius prosopis.*
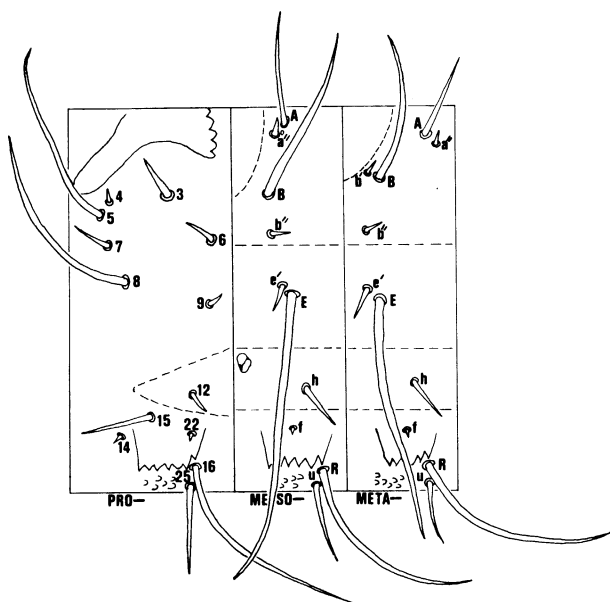
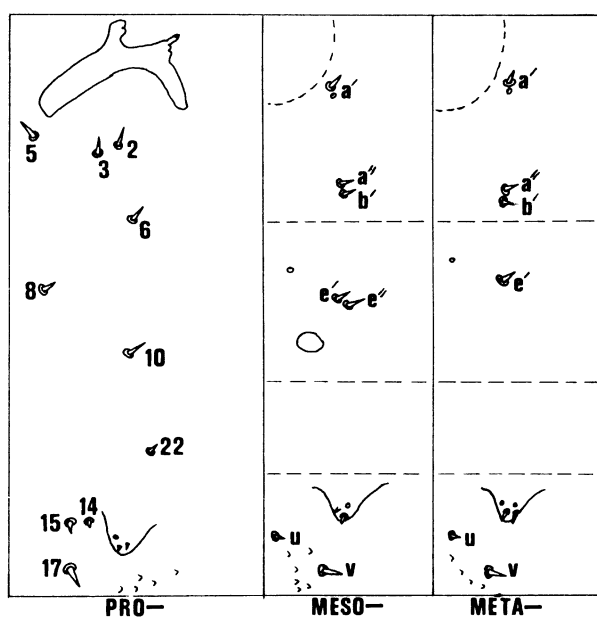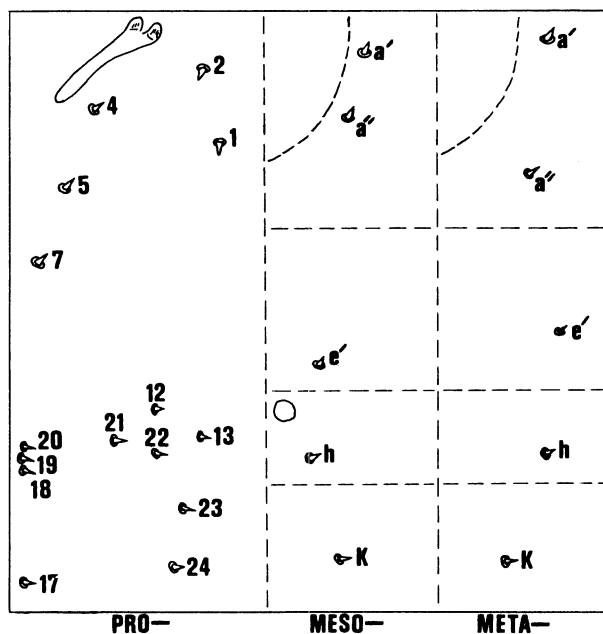FIGURE 11.—Thoracic setal map: *Amblycerus acapulcensis.*
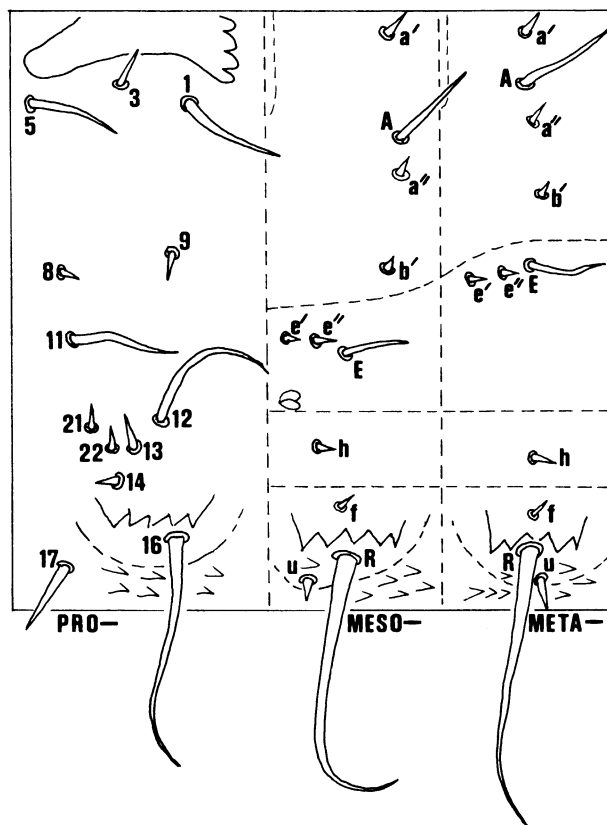
FIGURE 12.—Thoracic setal map: *Caryobruchus gleditsiae.*
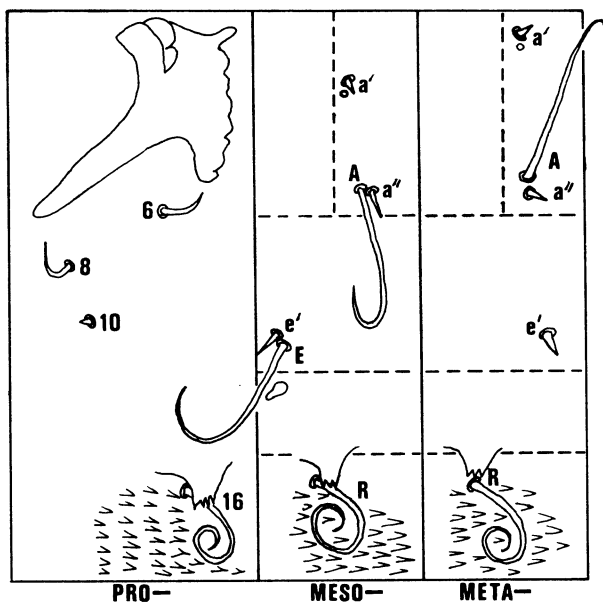
FIGURE 13.—Thoracic setal map: *Mimosestes amicus.*
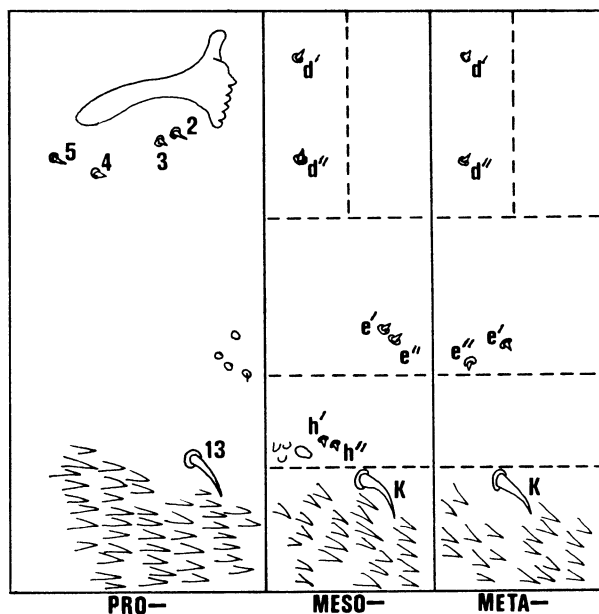
FIGURE 14.—Thoracic setal map: *Mimosestes protractus.*
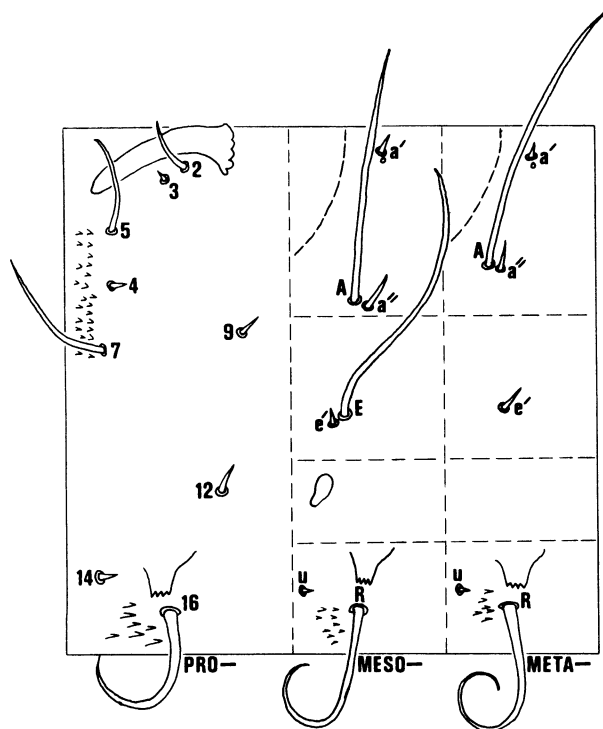
FIGURE 15.—Thoracic setal map: *Mimosestes sallaei.*
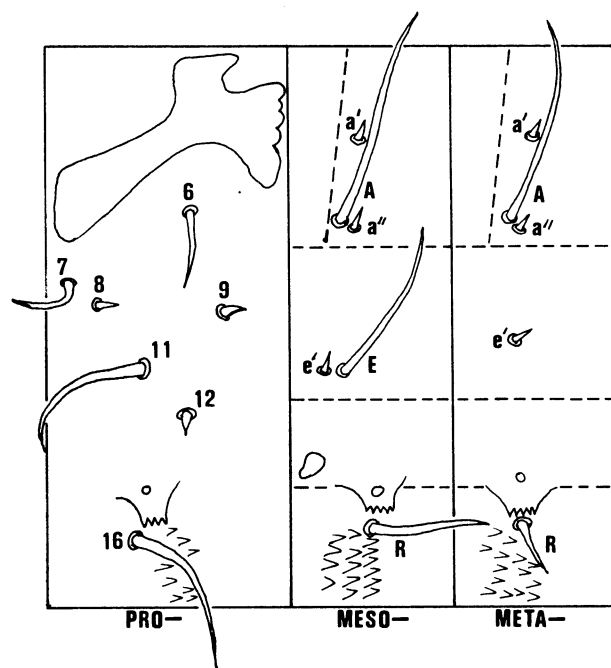
FIGURE 16.—Thoracic setal map: *Neltumius arizonensis.*
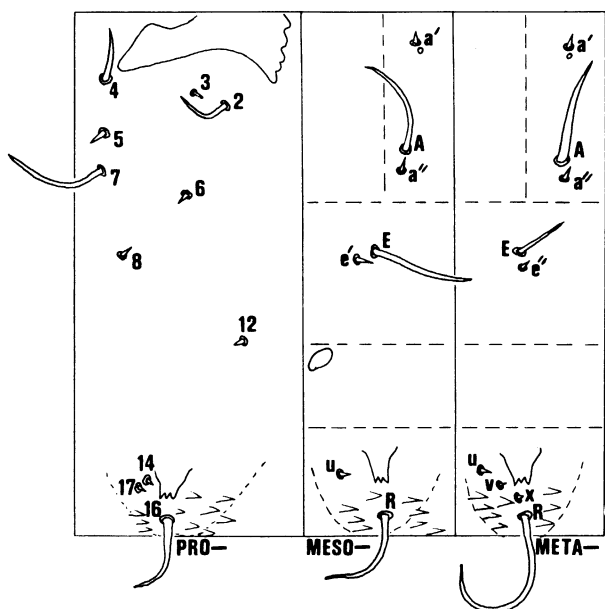
FIGURE 17.—Thoracic setal map: *Sennius morosus.*
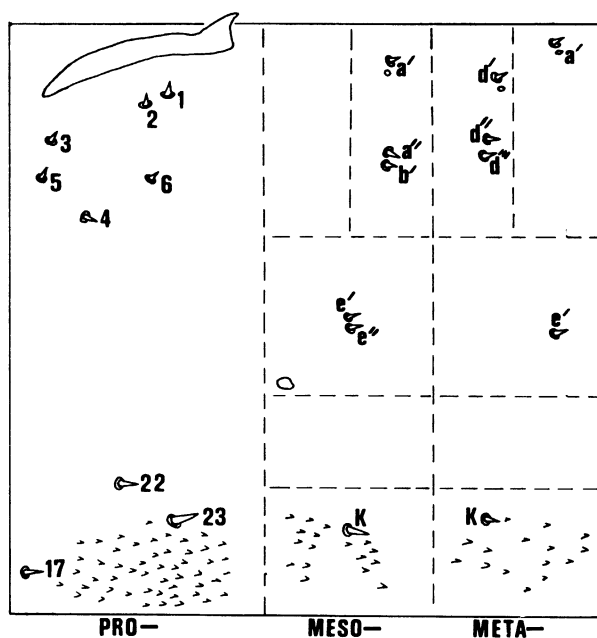
FIGURE 18.—Thoracic setal map: *Stator limbatus.*
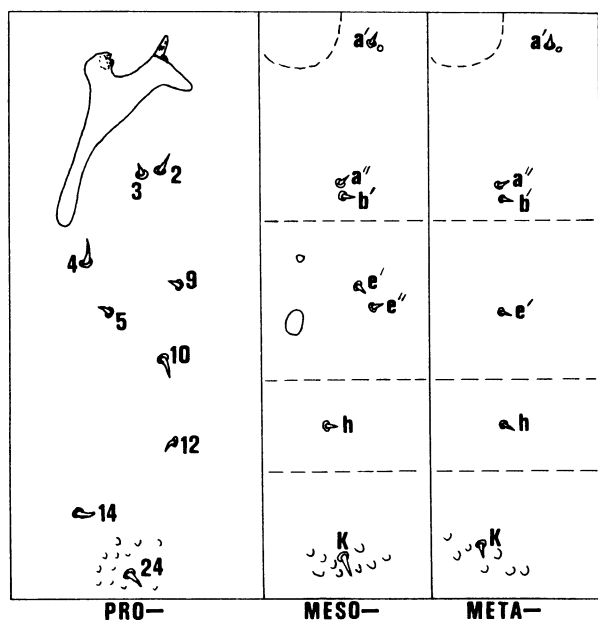
FIGURE 19.—Thoracic setal map: *Stator pruininus.*

FIGURE 20.—Thoracic setal map: *Stator pygidialis.*

FIGURE 21.—Thoracic setal map: *Zabrotes subfasciatus*.
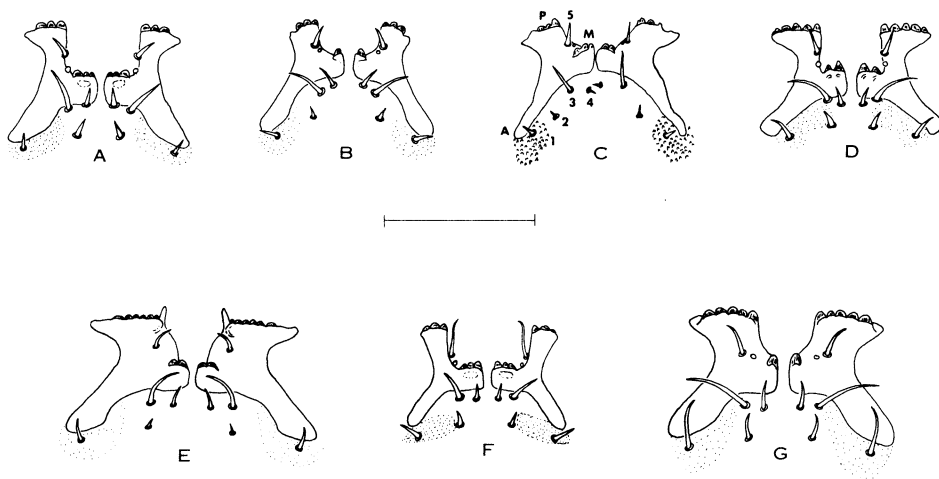
See legend at bottom of page 53.
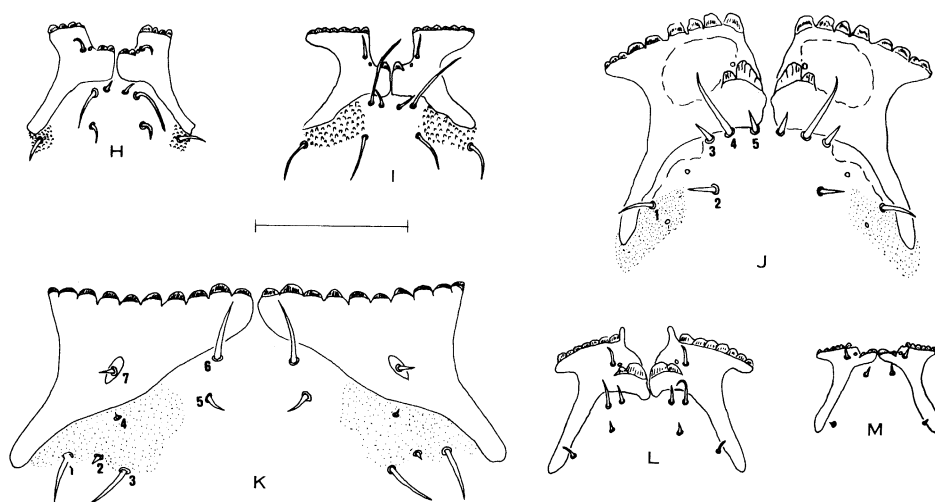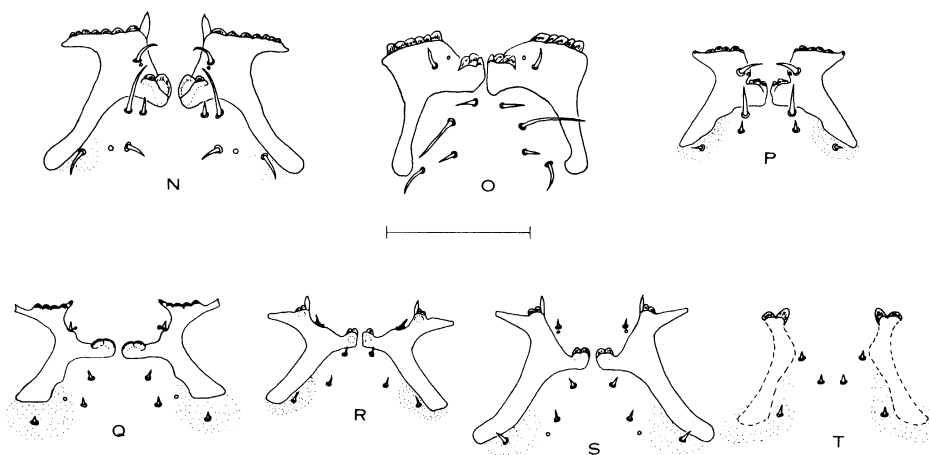
See legend at bottom of page.

FIGURE 22.—Prothoracic plates and associated setae: *A, Acanthoscelides aureolus*; *B, A. baboquivari*; *C, A. chiricahuae*; *D, A. collusus*; *E, A. macrophthalmus*; *F, A. mixtus*; *G, A. obtectus*; *H, Acanthoscelides prosopoides*; *I, Algarobius prosopis*; *J, Amblycerus acapulcensis*; *K, Caryobruchus gleditsiae*; *L, Mimosestes amicus*; *M, M. protractus*; *N, Mimosestes sallaei*; *O, Neltumius arizonensis*; *P, Sennius morosus*; *Q, Stator limbatus*; *R, S. pruininus*; *S, S. pygidialis*; *T, Zabrotes subfasciatus*. Scale line = 0.5 mm.
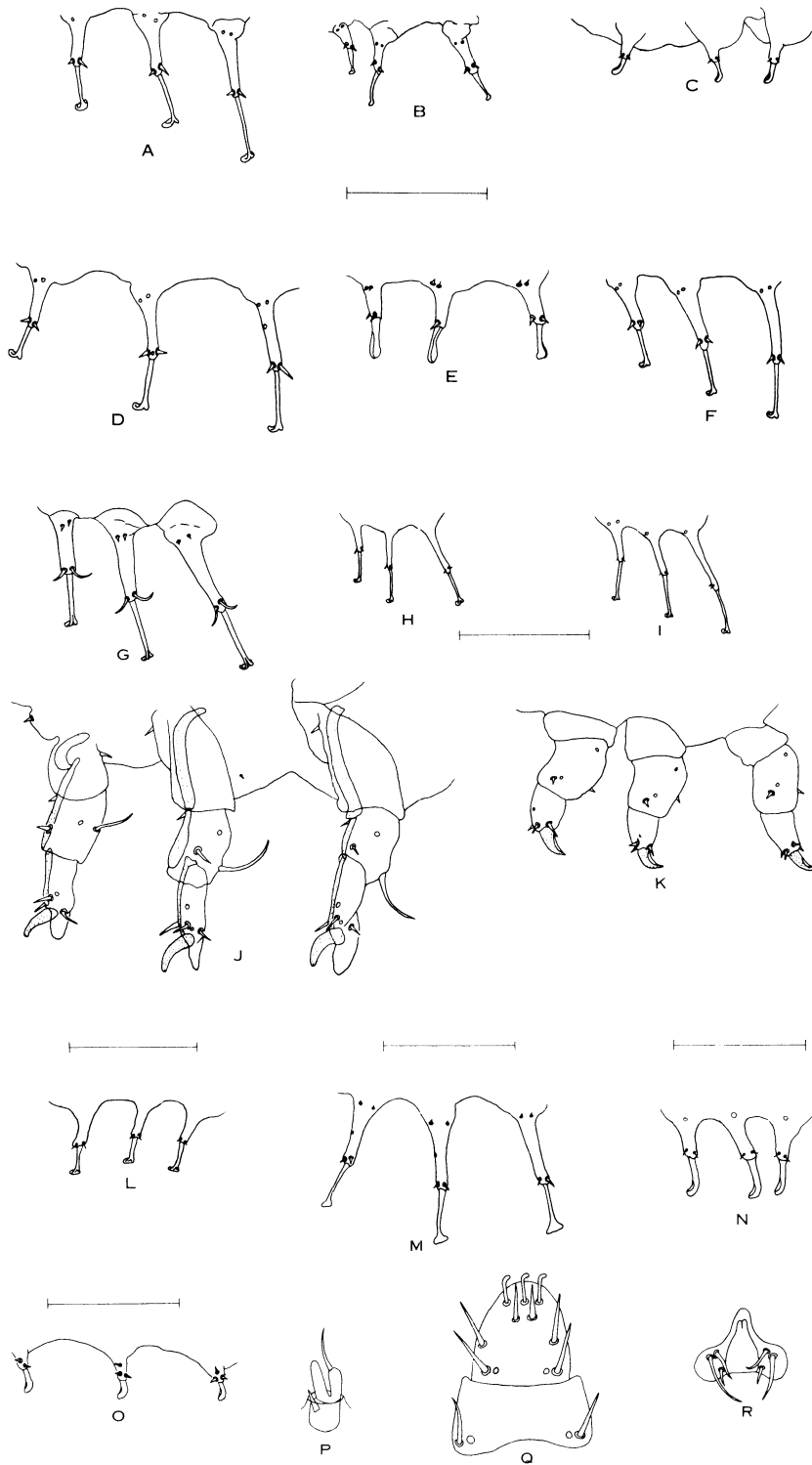
FIGURE 23.—Legs: *A, Acanthoscelides aureolus; B, A. baboquivari; C, A. chiricahuae; D, A. collusus; E, A. macrophthalmus; F, A. mixtus; G, Acanthoscelides obtectus; H, A. prosopoides; I, Algarobius prosopis; J, Amblycerus acapulcensis; K, Caryobruchus gleditsiae; L, Mimosestes amicus; M, M. sallaei; N, Neltumius arizonensis; O, Sennius morosus; P,* Antenna: *Algarobius prosopis; Q,* Clypeus-Labrum: *Mimosestes amicus; R,* Labium: *M. amicus.* Scale line = 0.25 mm.
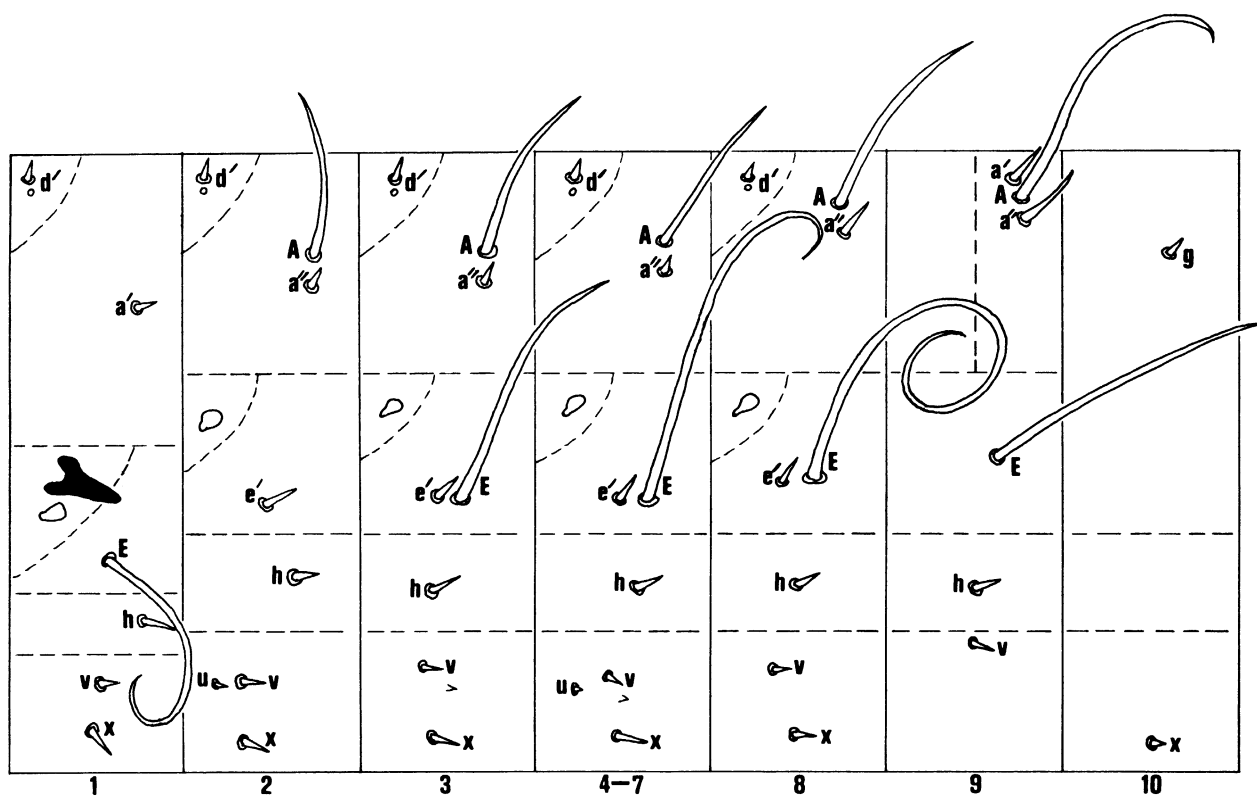
FIGURE 24.—Abdominal setal map of *Acanthoscelides aureolus.*
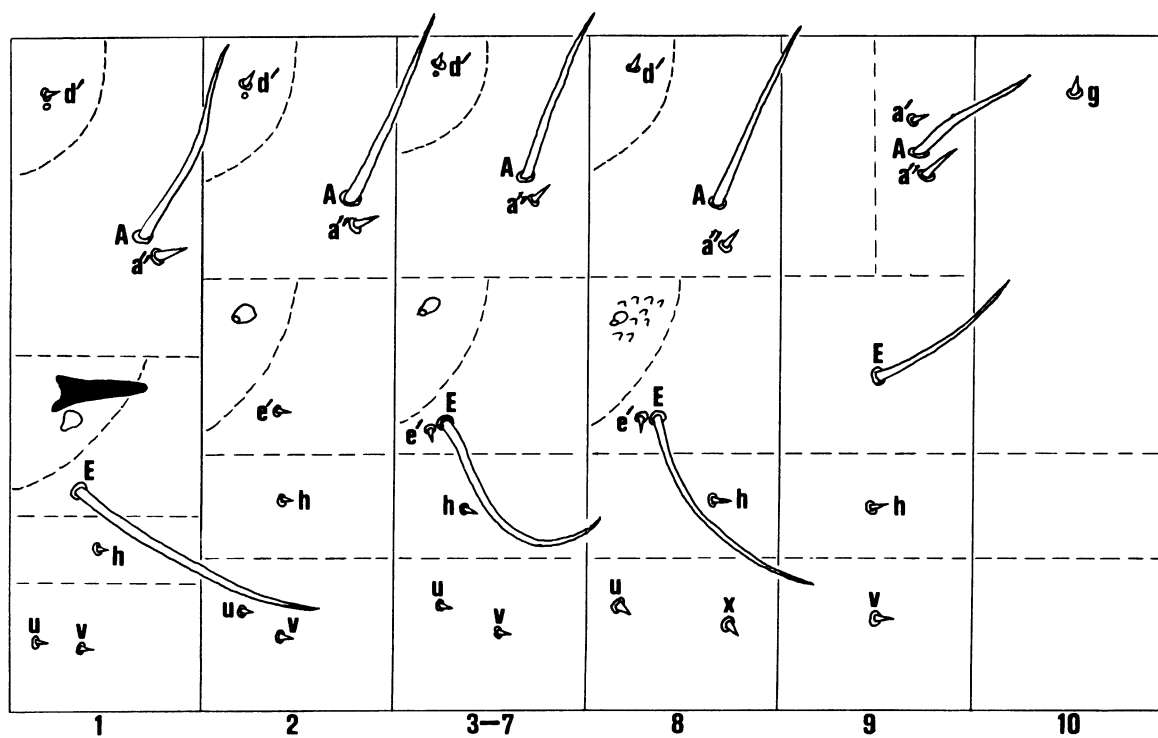
FIGURE 25.—Abdominal setal map of *Acanthoscelides baboquivari.*
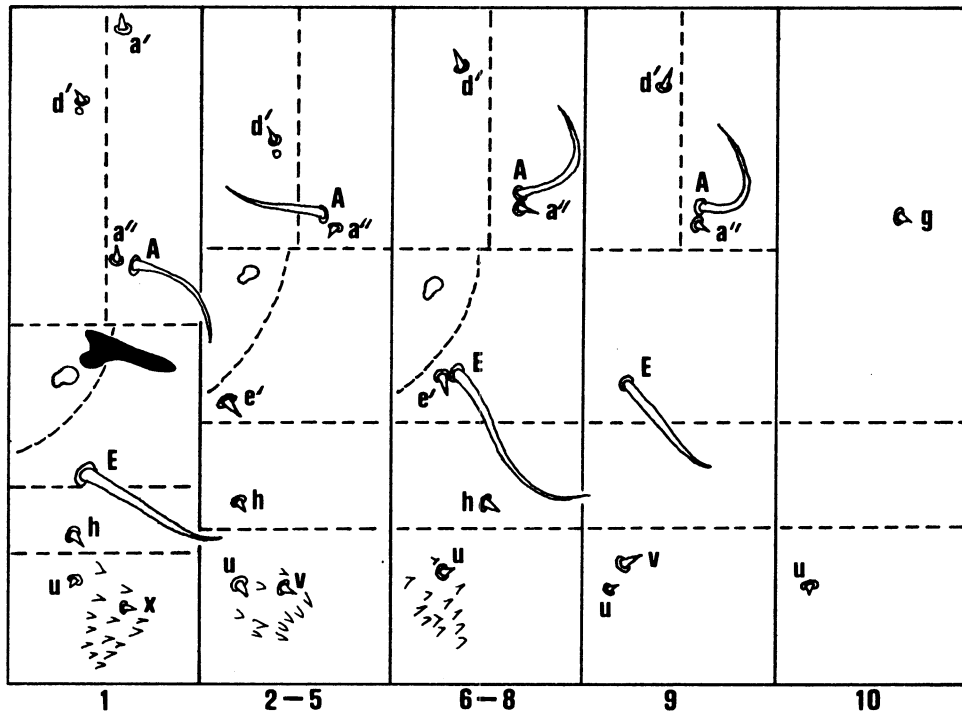
FIGURE 26.—Abdominal setal map of *Acanthoscelides chiricahuae.*
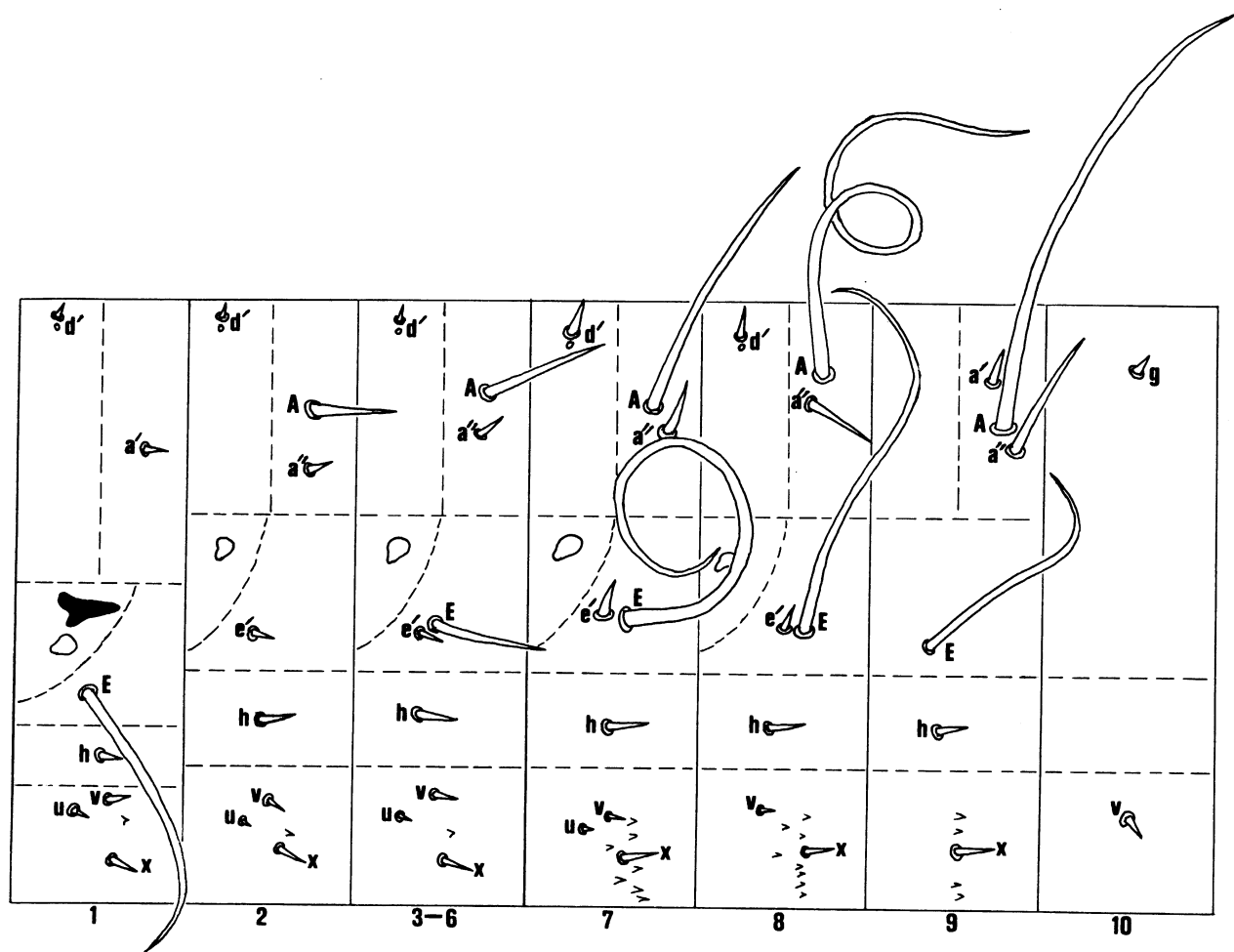
FIGURE 27.—Abdominal setal map of *Acanthoscelides collusus*.
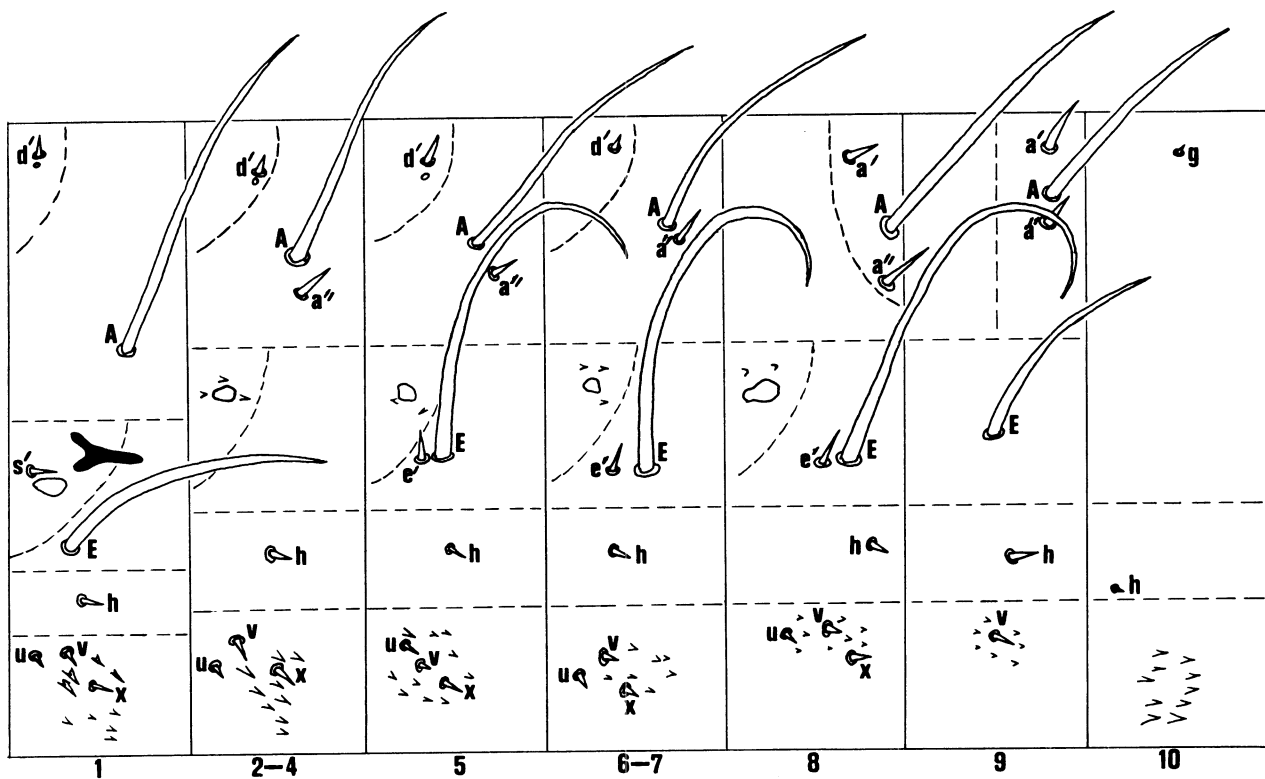
FIGURE 28.—Abdominal setal map of *Acanthoscelides macrophthalmus*.
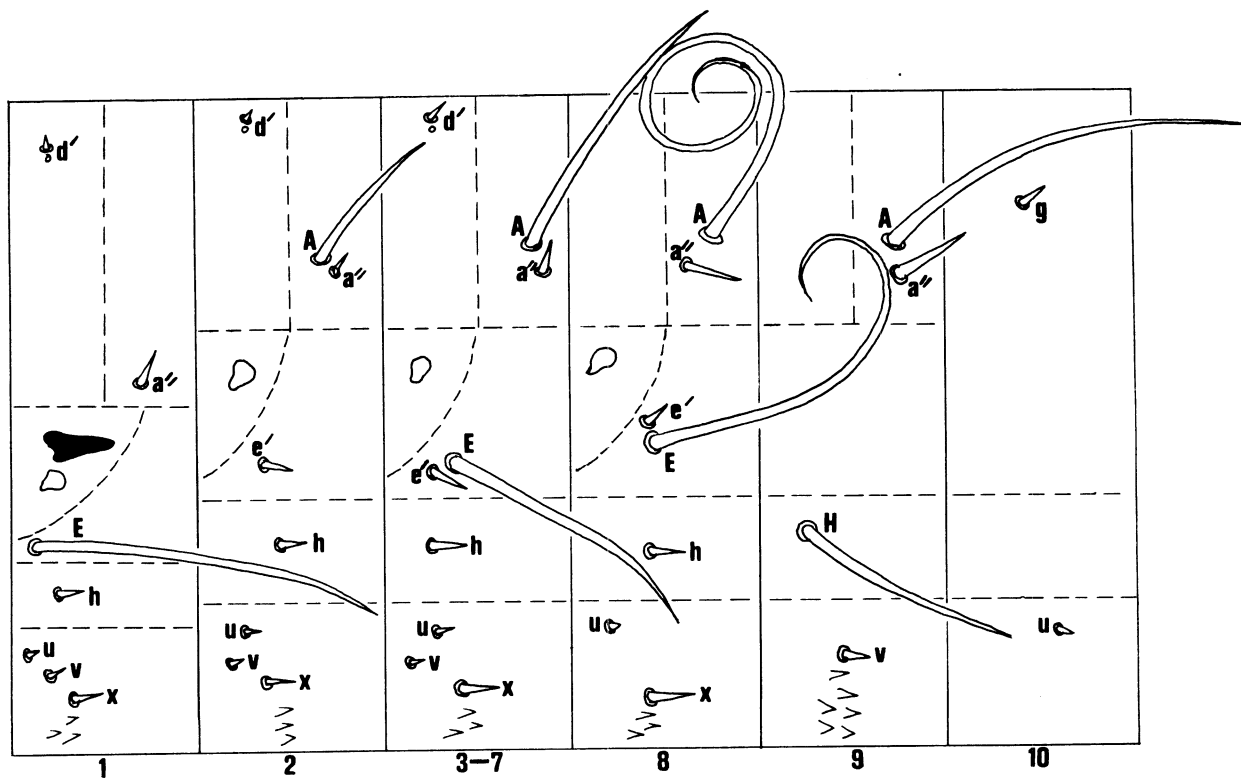
FIGURE 29.—Abdominal setal map of *Acanthoscelides mixtus*.
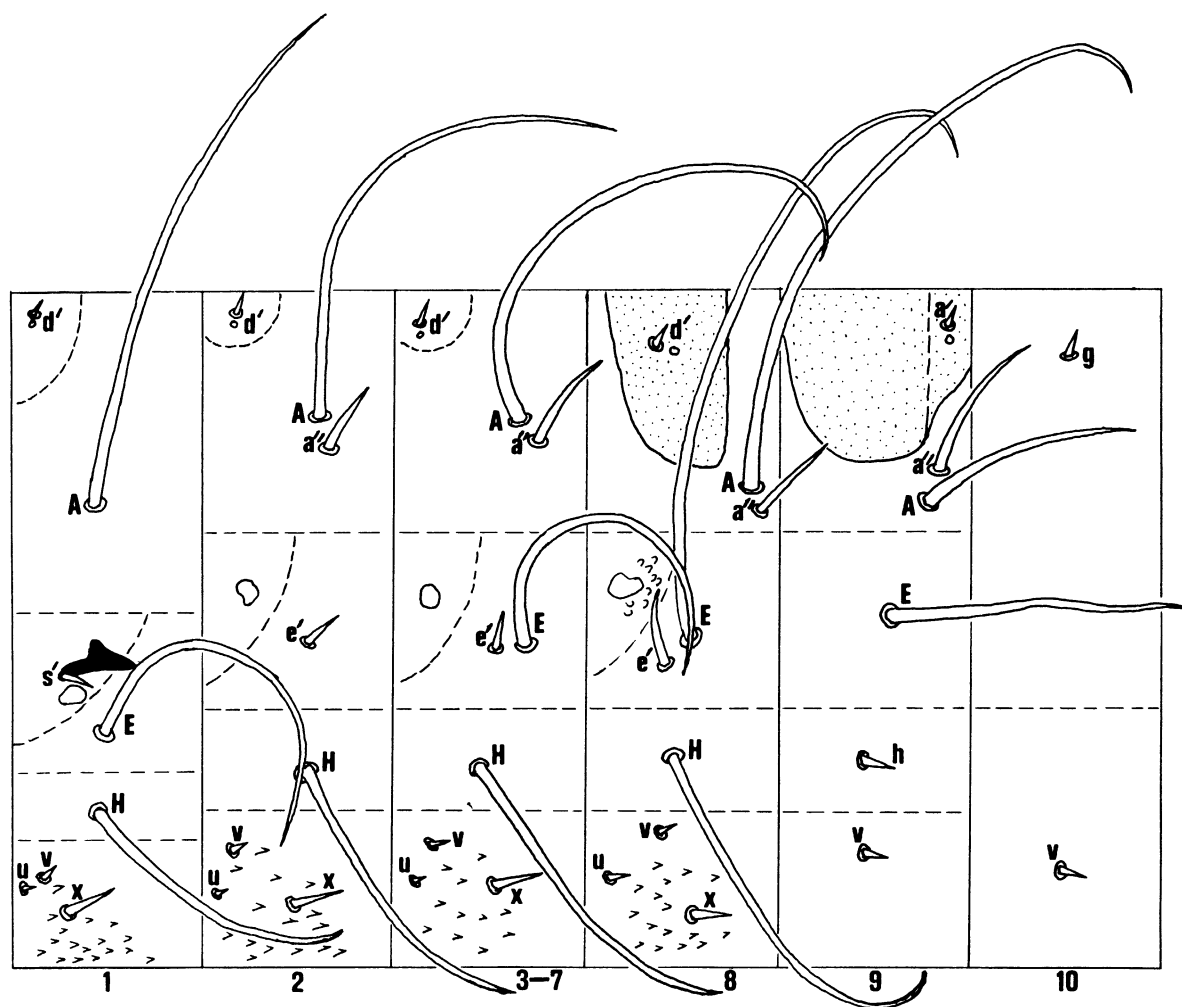
FIGURE 30.—Abdominal setal map of *Acanthoscelides obtectus.*
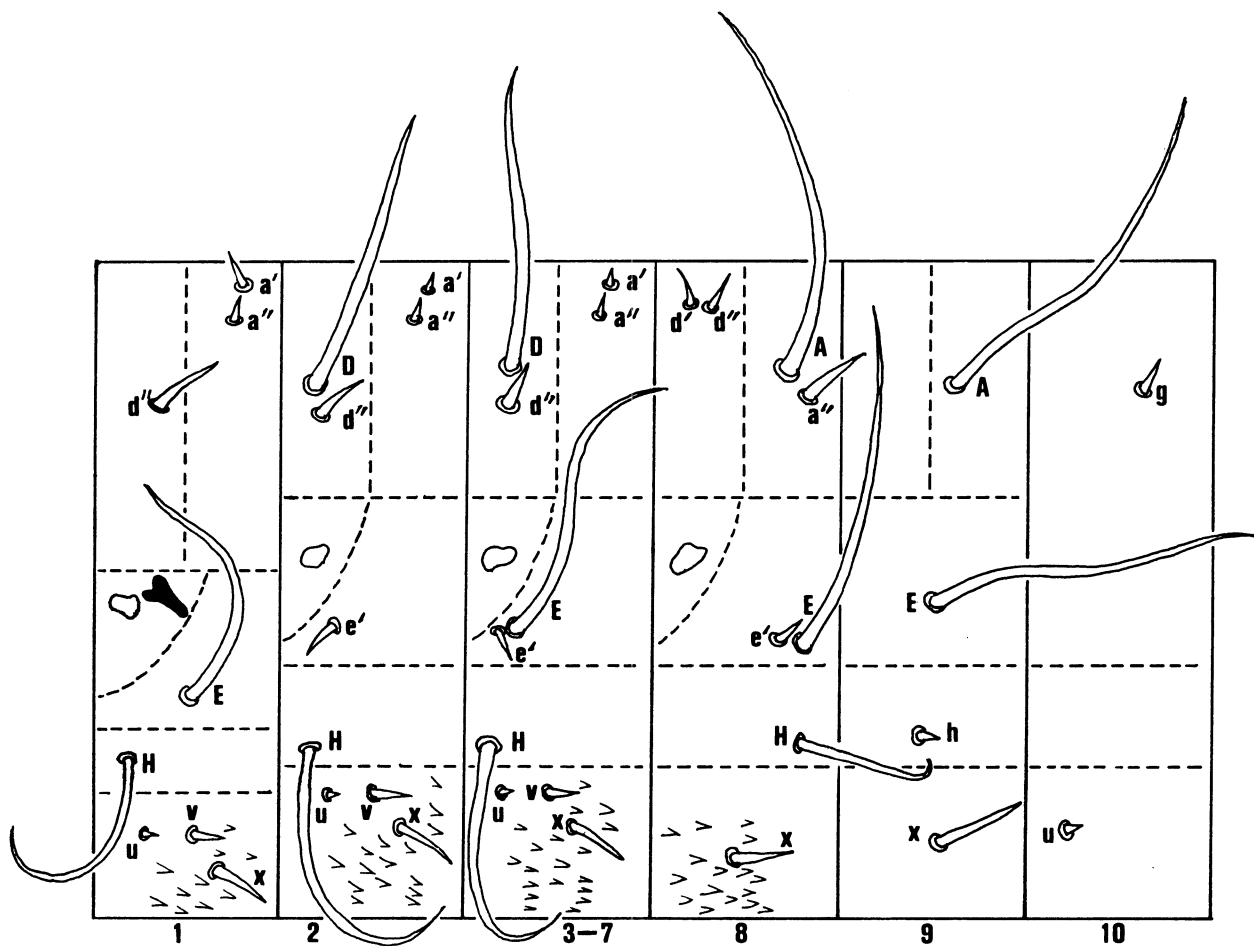
FIGURE 31.—Abdominal setal map of *Acanthoscelides prosopoides*.
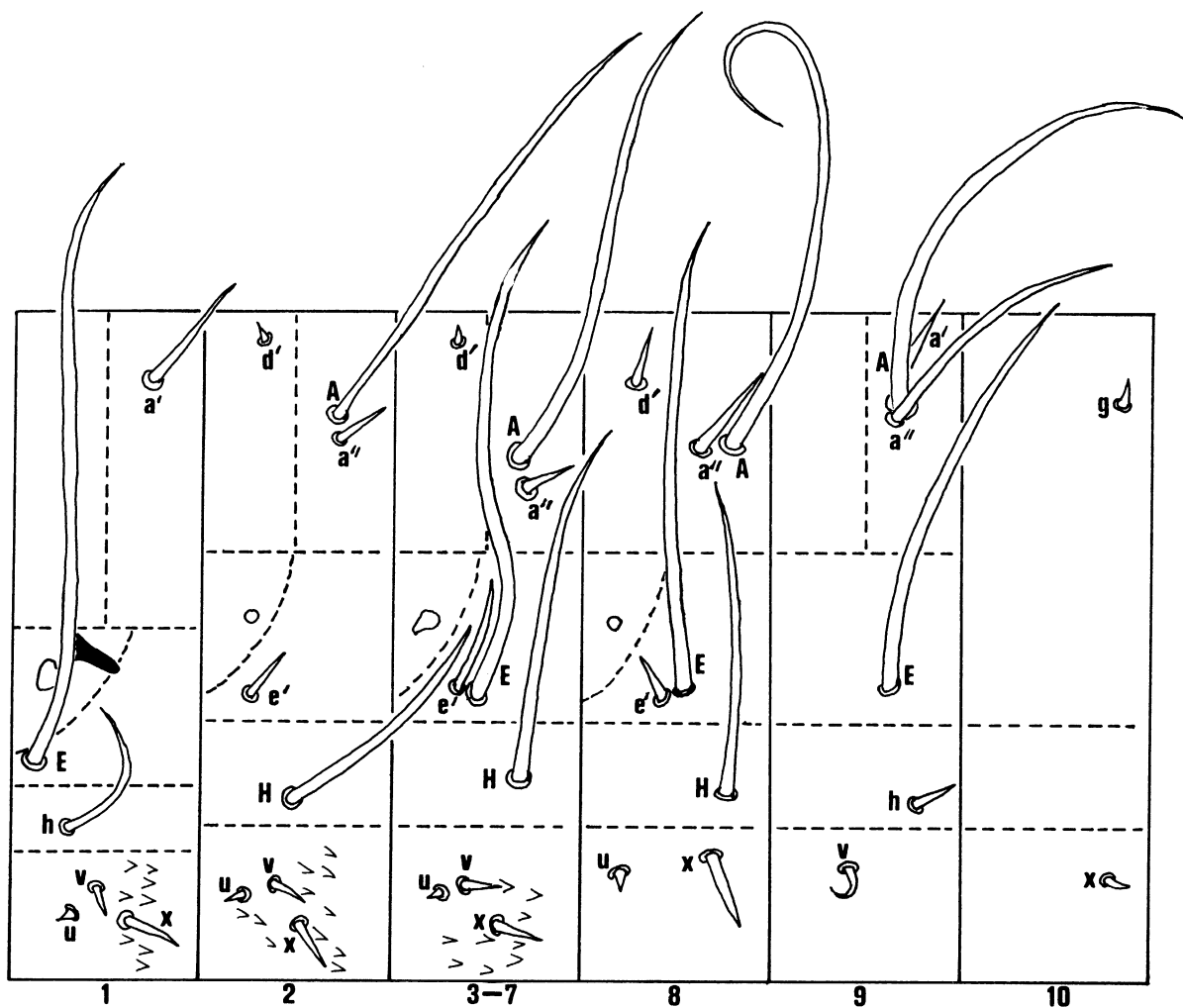
FIGURE 32.—Abdominal setal map of *Algarobius prosopis*.
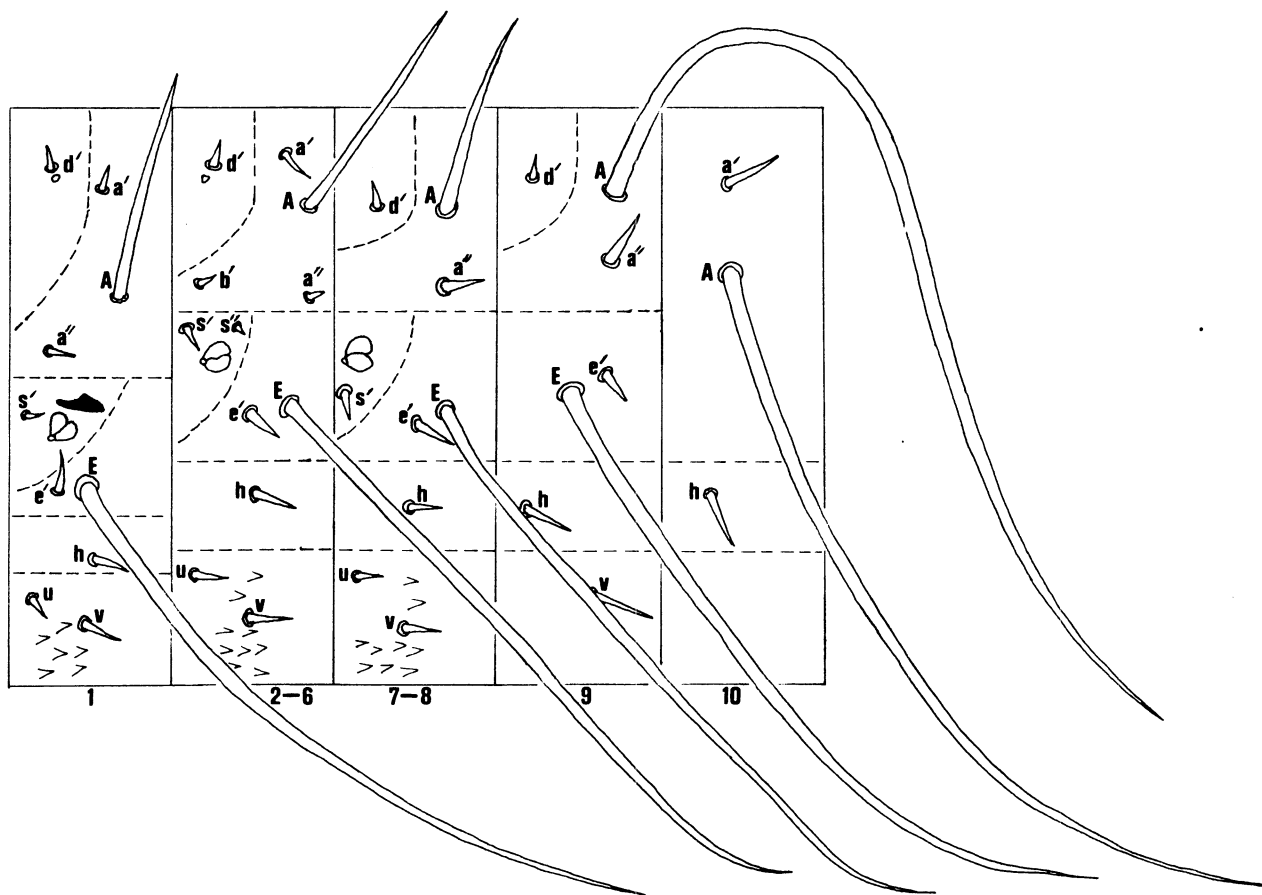
FIGURE 33.—Abdominal setal map of *Amblycerus acapulcensis*.
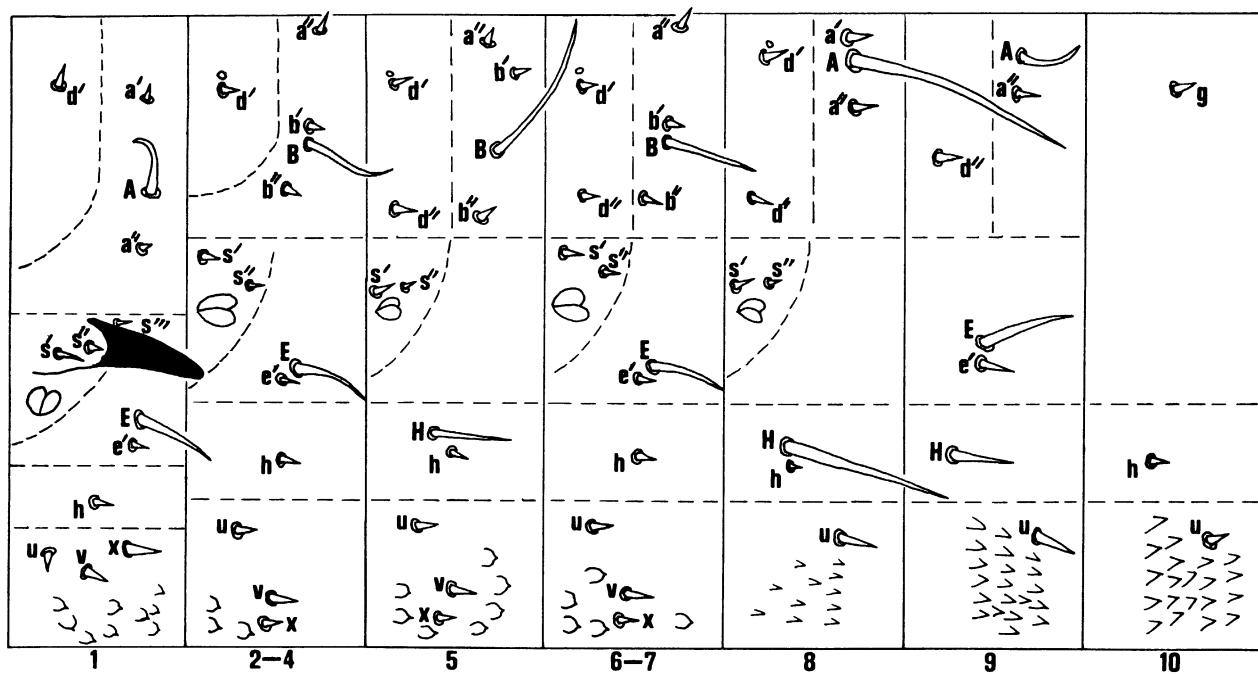
FIGURE 34.—Abdominal setal map of *Caryobruchus gleditsiae*.
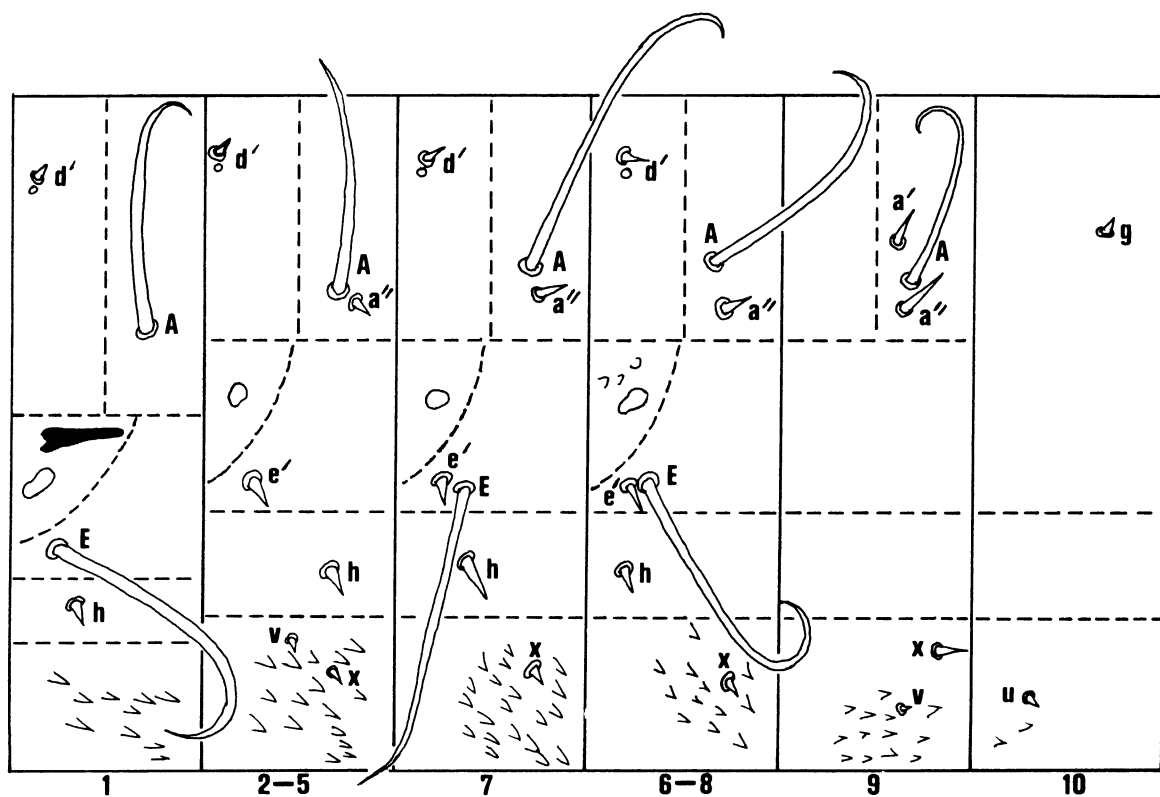
FIGURE 35.—Abdominal setal map of *Mimosestes amicus*.
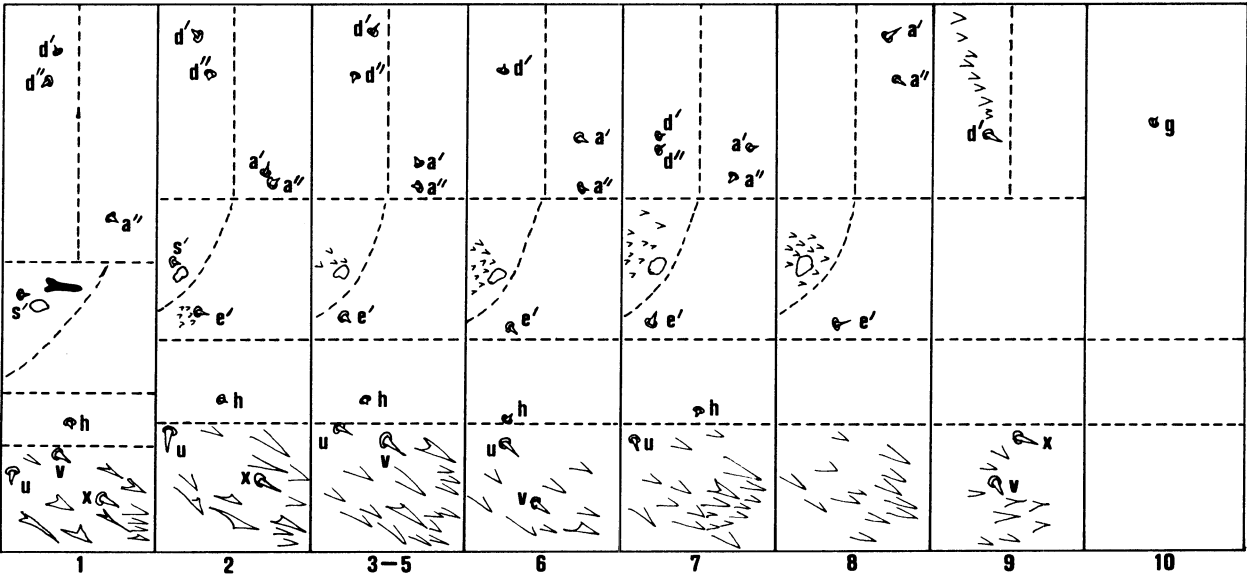
FIGURE 36.—Abdominal setal map of *Mimosestes protractus*.
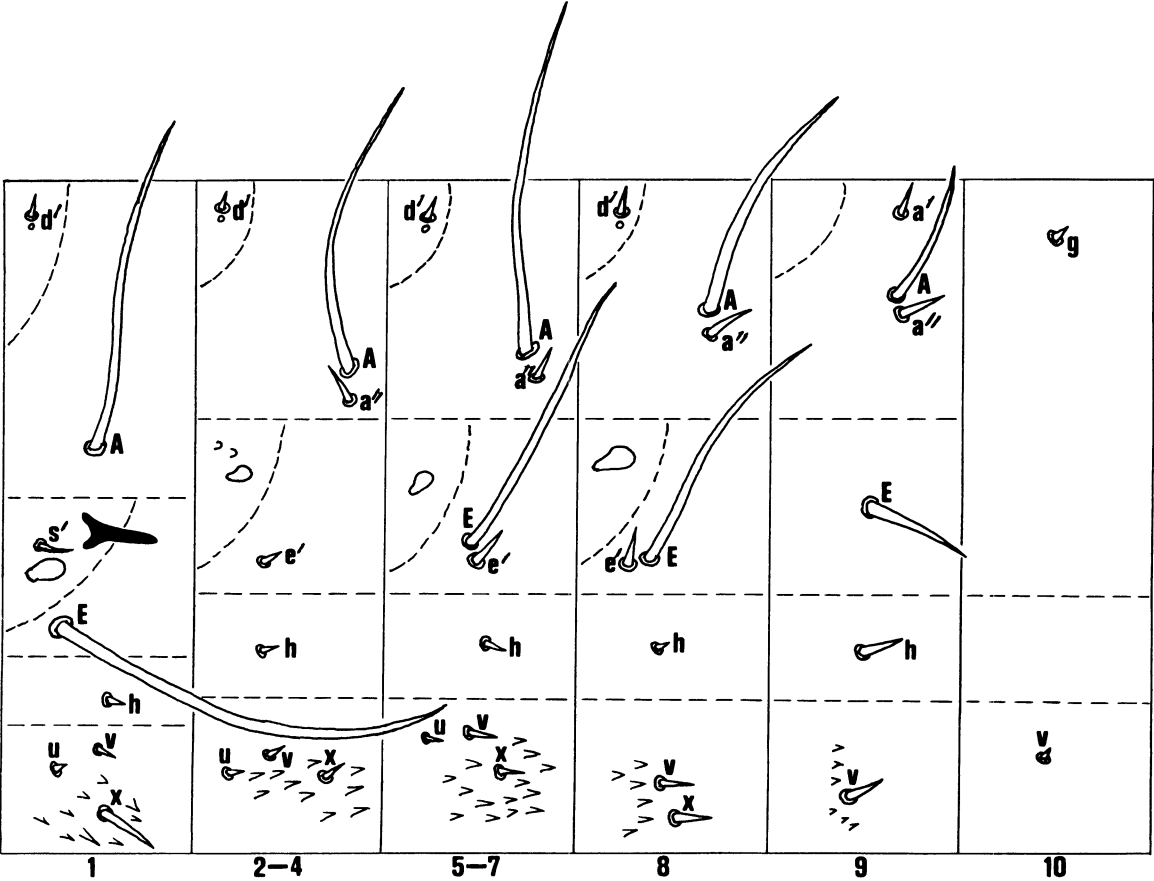
FIGURE 37.—Abdominal setal map of *Mimosestes sallaei*.
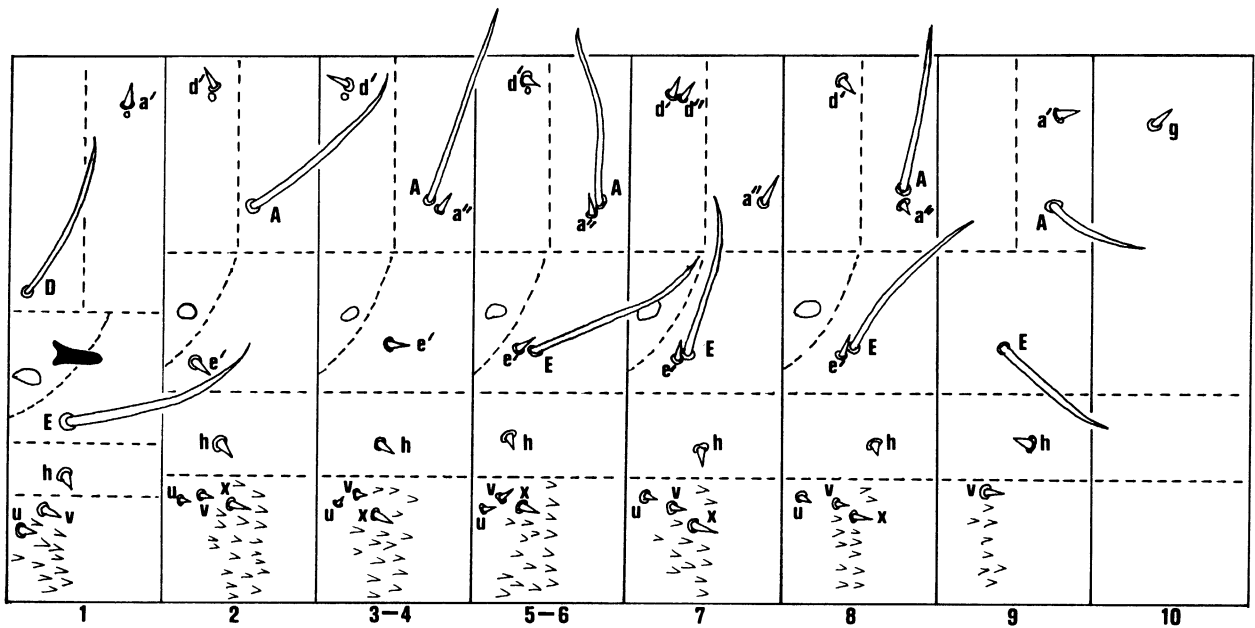
FIGURE 38.—Abdominal setal map of *Neltumius arizonensis*.
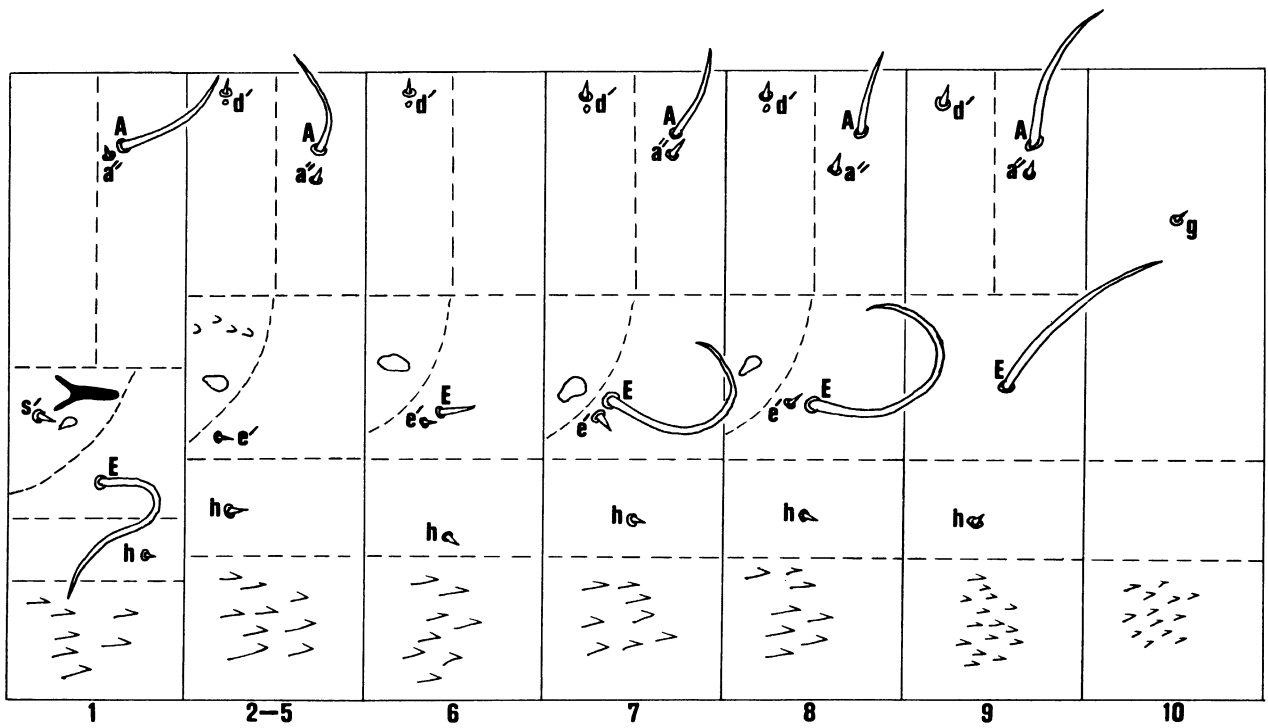
FIGURE 39.—Abdominal setal map of *Sennius morosus*.
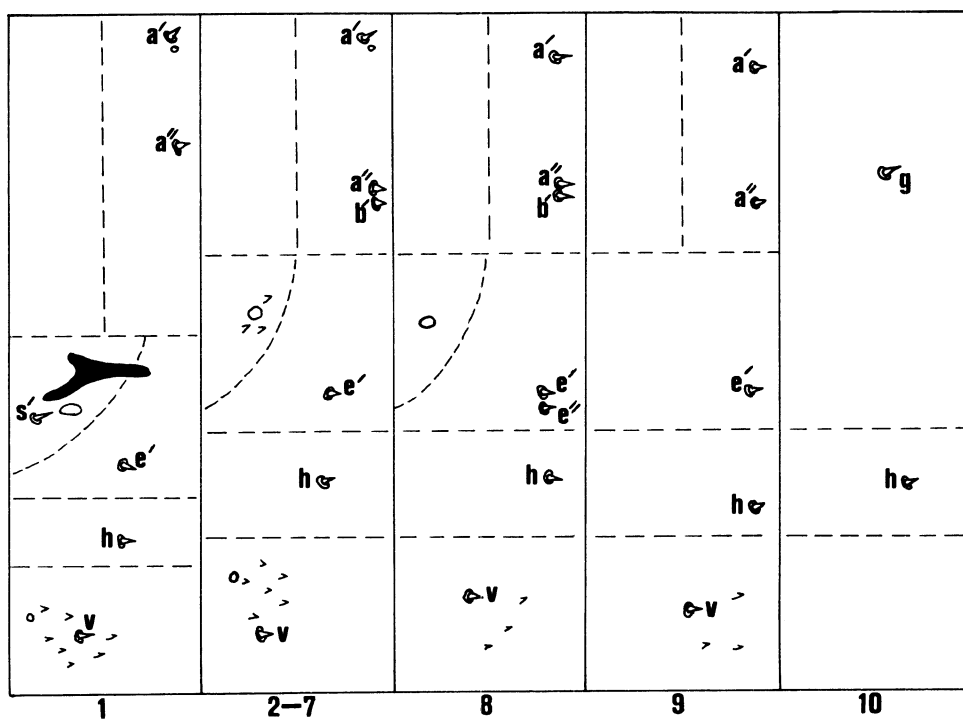
FIGURE 40.—Abdominal setal map of *Stator limbatus*.
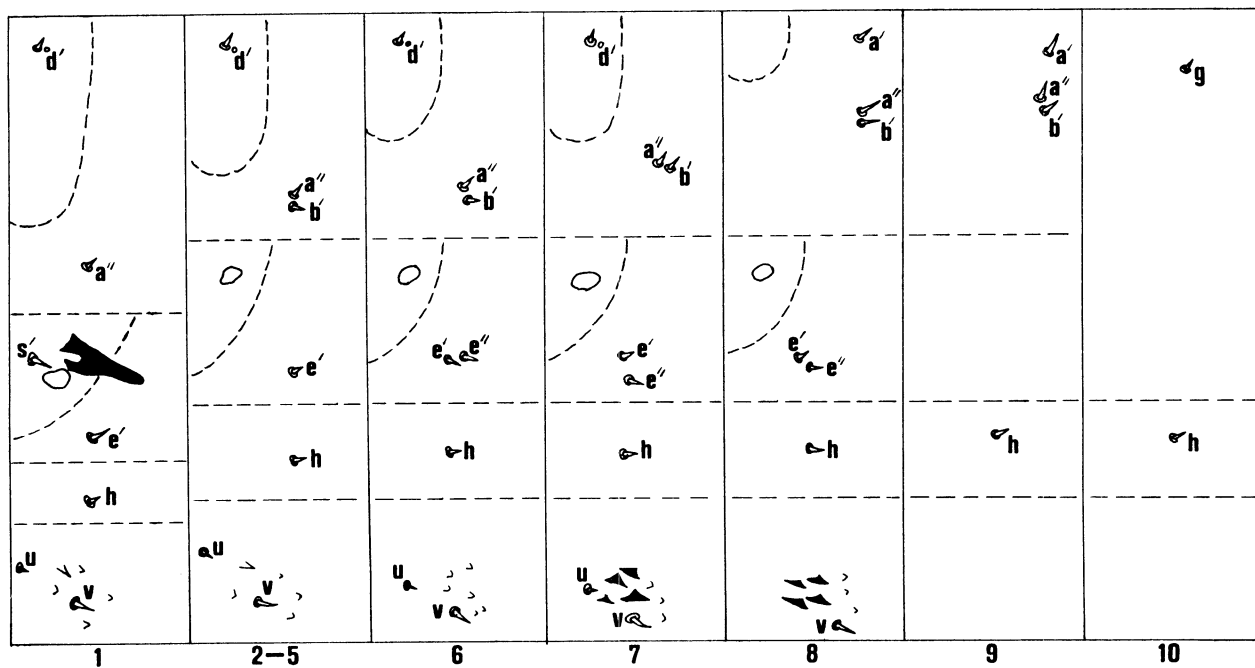
FIGURE 41.—Abdominal setal map of *Strator pruininus*.
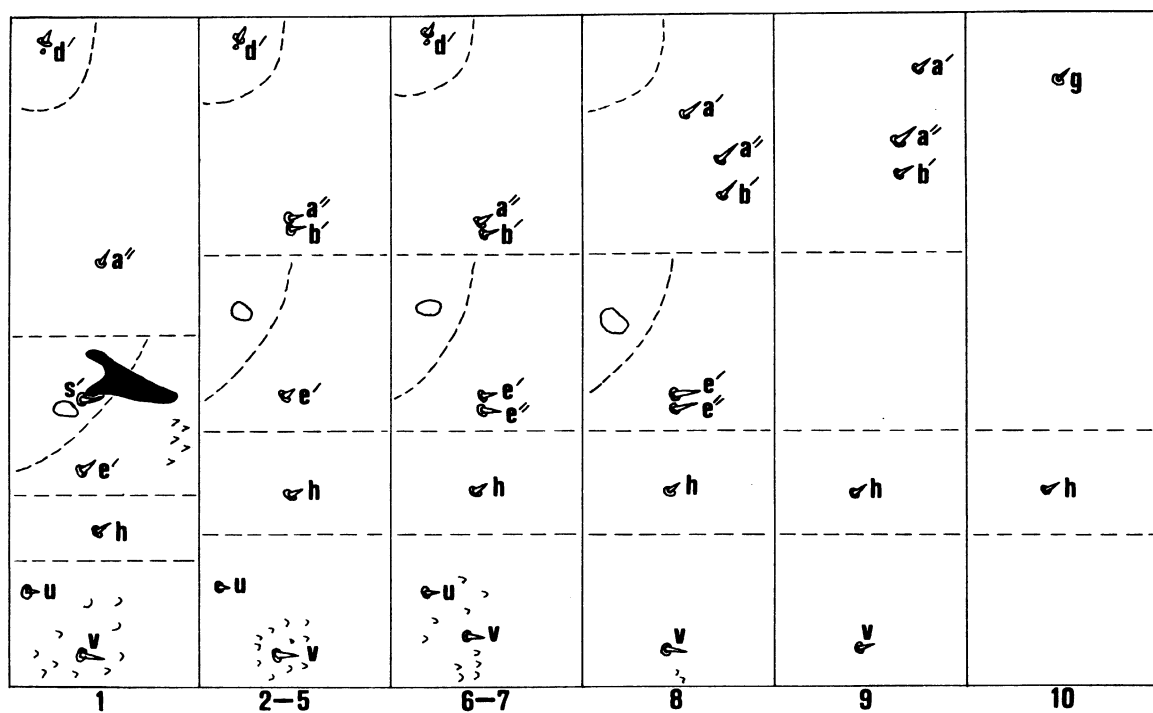
FIGURE 42.—Abdominal setal map of *Stator pygidialis*.
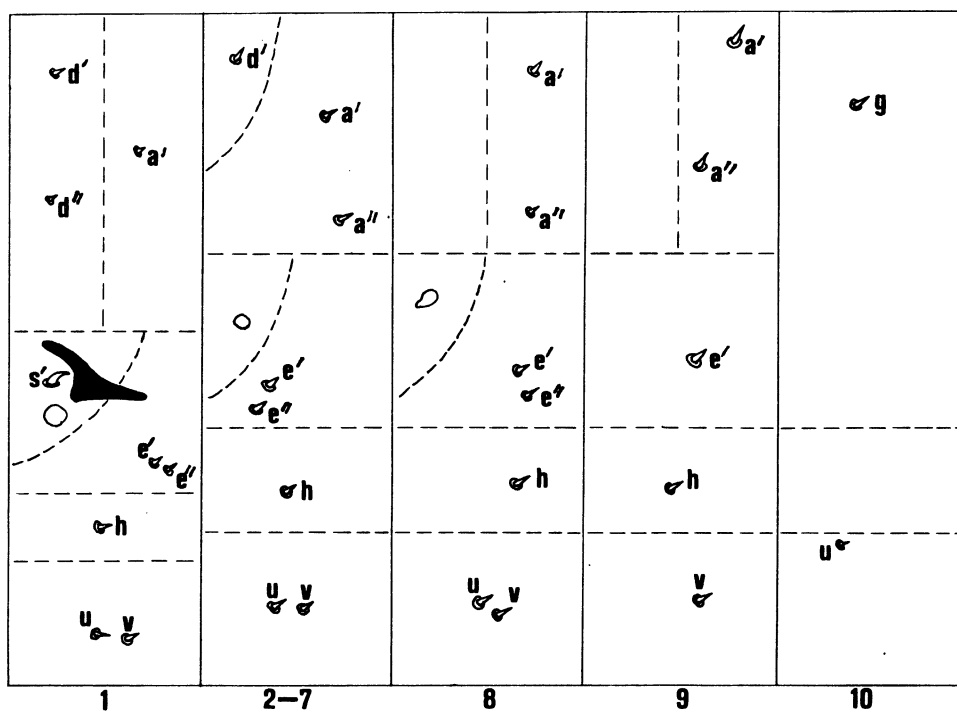
FIGURE 43.—Abdominal setal map of *Zabrotes subfasciatus*.
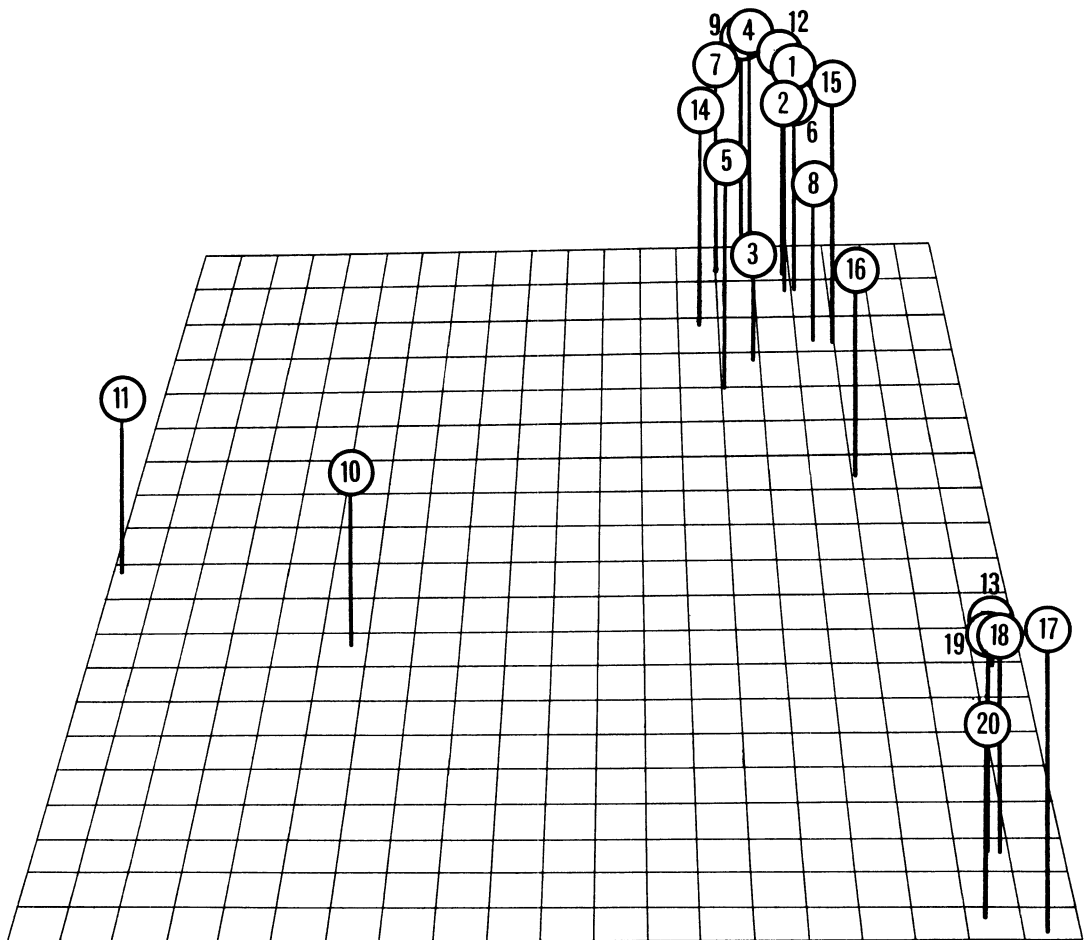
FIGURE 44.—Principal Component Analysis showing phenetic relationships between first instar larvae. 1, *Acanthoscelides aureolus*; 2, *A. baboquivari*; 3, *A. chiricahuae*; 4, *A. collusus*; 5, *A. macrophthalmus*; 6, *A. mixtus*; 7, *A. obtectus*; 8, *A. prosopoides*; 9, *Algarobius prosopis*; 10, *Amblycerus acapulcensis*; 11, *Caryobruchus gleditsiae*; 12, *Mimosestes amicus*; 13, *M. protractus*; 14, *M. sallaei*; 15, *Neltumius arizonensis*; 16, *Sennius morosus*; 17, *Stator limbatus*; 18, *S. pruininus*; 19, *S. pygidialis*; 20, *Zabrotes subfasciatus*.
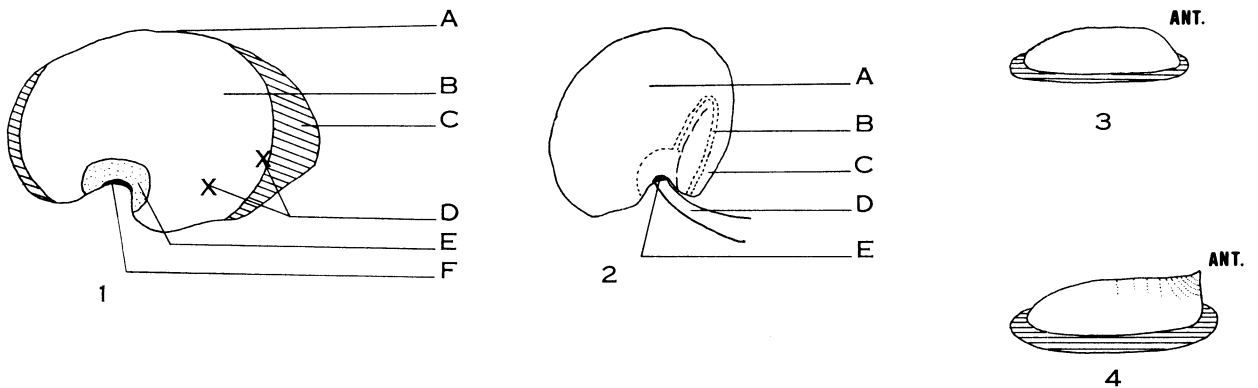
FIGURE 45.—1. Seed of *Astragalus praelongus* showing: *A*, Integument; *B*, chamber excavated by larva; *C*, cotyledon tissue remaining after feeding by fourth instar; *D*, sites of oviposition and larval entry; *E*, seedcoat tissue; *F*, hilum. 2. Seed of *Astragalus wootoni* showing: *A*, Cotyledons; *B*, burrow of first instar larva; *C*, radicle; *D*, funiculus; *E*, hilum. 3. Egg of *Stator limbatus* or *S. pruininus*. 4. Egg of *Stator pygidialis*.

APPENDIX TABLES

TABLE 1.—*Distribution of setae on* Acanthoscelides aureolus, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area[1]	Epi-pleu-ron	Hypo-pleu-ron	Sternum		Prothorax
Mesothorax	d′	A a″		Ee′		u	R	2
Metathorax	d′	A a″		e′		u	R	3
Abdomen								4
1	d′	a′		E	h	vx		5
2	d′	A a″		e′	h	uvx		6
3	d′	A a″		Ee′	h	vx		7
4–7	d′	A a″		Ee′	h	uvx		12
8	d′	A a″		Ee′	h	vx		14
9		Aa′a″		E	h	v		16
10	g[2]						x	17

[1] None present in species.
[2] Dorsolateral seta on abdominal segment 10.

TABLE 2.—*Distribution of setae on* Acanthoscelides baboquivari, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area[1]	Epi-pleu-ron	Hypo-pleu-ron	Sternum		Prothorax	
Mesothorax		Aa′a″		Ee′		uf	R	2	16
Metathorax		Aa′a″		e′		uf	R	3	
Abdomen								4	
1	d′	A a″		E	h	uv		5	
2	d′	A a″		e′	h	uv		6	
3–7	d′	A a″		Ee′	h	uv		8	
8	d′	A a″		Ee′	h	u x		12	
9		Aa′a″		E	h	v		14	
10	g[2]							15	

[1] None present in species.
[2] Dorsolateral seta on abdominal segment 10.

TABLE 3.—*Distribution of setae on* Acanthoscelides chiricahuae, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area[1]	Epi-pleu-ron	Hypo-pleu-ron	Sternum		Prothorax	
Mesothorax		a″		Ee′	H	u	R	1	16
Metathorax		a″		Ee′	Hh	u	R	6	
Abdomen								8	
1	d′	Aa′a″		E	h	u x		9	
2–5	d′	A a″		e′	h	uv		10	
6–8	d′	A a″		Ee′	h	u		11	
9	d′	A a″		E		uv		12	
10	g[2]						u	14	

[1] None present in species.
[2] Dorsolateral seta on abdominal segment 10.

TABLE 4.—*Distribution of setae on* Acanthoscelides collusus, *first instar*

Segment	Pro-dorsum	Post-dorsum	Spiracular area[1]	Epi-pleuron	Hypo-pleuron	Sternum	Prothorax
Mesothorax	Dd'd"			Ee'		u	R 2 17
Metathorax	Dd'd"			e'		u	R 3
Abdomen							4
1	d'	a'		E	h	uvx	5
2	d'	A a"		e'	h	uvx	6
3–7	d'	A a"		Ee'	h	uvx	7
8	d'	A a"		Ee'	h	vx	12
9		Aa'a"		E	h	x	14
10 g²						v	16

[1] None present in species.
[2] Dorsolateral seta on abdominal segment 10.

TABLE 5.—*Distribution of setae on* Acanthoscelides macrophthalmus, *first instar*

Segment	Pro-dorsum	Post-dorsum	Spiracular area	Epi-pleuron	Hypo-pleuron	Sternum	Prothorax
Mesothorax	Dd'd"			Ee'		u	R 2
Metathorax	Dd'd"			e'			R 3
Abdomen							4
1	d'	A	s'	E	h	uvx	5
2–4	d'	A a"			h	uvx	8
5–7	d'	A a"		Ee'	h	uvx	9
8		Aa'a"		Ee'	h	uvx	12
9		Aa'a"		E	h	v	14
10 g¹					h		16

[1] Dorsolateral seta on abdominal segment 10.

TABLE 6.—*Distribution of setae on* Acanthoscelides mixtus, *first instar*

Segment	Pro-dorsum	Post-dorsum	Spiracular area[1]	Epi-pleuron	Hypo-pleuron	Sternum	Prothorax
Mesothorax	d'	A a"		Ee'		u	R 1
Metathorax	d'	A a"		e'		u	R 2
Abdomen							3
1	d'	a"		E	h	uvx	4
2	d'	A a"		e'	h	uvx	5
3–7	d'	A a"		Ee'	h	uvx	7
8		A a"		Ee'	h	u x	11
9		A a"			H	v	15
10 g²						u	16

[1] None present in species.
[2] Dorsolateral seta on abdominal segment 10.

TABLE 7.—*Distribution of setae on* Acanthoscelides obtectus, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area	Epi-pleu-ron	Hypo-pleu-ron	Sternum		Prothorax	
Mesothorax	D d″	a′		Ee′		u	R	2	16
Metathorax	D d″	a′		e′		u	R	3	
Abdomen								4	
1	d′	A	s′	E	H	uvx		5	
2	d′	A a″		e′	H	uvx		6	
3–8	d′	A a″		Ee′	H	uvx		9	
9		Aa′a″		E	h	v		12	
10 g¹						v		14	

[1] Dorsolateral seta on abdominal segment 10.

TABLE 8.—*Distribution of setae on* Acanthoscelides prosopoides, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area[1]	Epi-pleu-ron	Hypo-pleu-ron	Sternum		Prothorax
Mesothorax	Dd′d″				Hh	u	R	4
Metathorax	Dd′d″			e′		u	R	5
Abdomen								8
1	d′	a′a″ ،		E	H	uvx		11
2	D d″	a′a″		e′	H	uvx		12
3–7	D d″	a′a″		Ee′	H	uvx		14
8	d′d″	A a″		Ee′	H	x		15
9		A		E	h	x		16
10 g²						u		

[1] None present in species.
[2] Dorsolateral seta on abdominal segment 10.

TABLE 9.—*Distribution of setae on* Algarobius prosopis, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area[1]	Epi-pleu-ron	Hypo-pleu-ron	Sternum		Prothorax
Mesothorax		A a″		Ee′		u	R	1
Metathorax		Aa′a″		e′		u	R	4
Abdomen								5
1		a′		E	h	uvx		6
2	d′	A a″		e′	H	uvx		9
3–7	d′	A a″		Ee′	H	uvx		14
8	d′	A a″		Ee′	H	u x		15
9		Aa′a″		E	h	v		16
10 g²						x		

[1] None present in species.
[2] Dorsolateral seta on abdominal segment 10.

TABLE 10.—*Distribution of setae on* Amblycerus acapulcensis, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area	Epi-pleu-ron	Hypo-pleu-ron	Sternum		Prothorax	
Mesothorax		A a″B b″		Ee′	h	uf	R	3	14
Metathorax		A a″Bb′b″		Ee′	h	uf	R	4	15
Abdomen								5	16
1	d′	Aa′a″	s′	Ee′	h	uv		6	22
2–6	d′	Aa′a″b′	s′s″	Ee′	h	uv		7	25
7–8	d′	A a″	s′		h	uv		8	
9	d′	A a″		Ee′	h	v		9	
10		Aa′			h			12	

TABLE 11.—*Distribution of setae on* Caryobruchus gleditsiae, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area	Epi-pleu-ron	Hypo-pleu-ron	Sternum		Prothorax	
Mesothorax		Aa′a″ b′		Ee′e″	h	uf	R	1	17
Metathorax		Aa′a″ b′		Ee′e″	h	uf	R	3	21
Abdomen								5	22
1	d′	Aa′a″	s′s″s‴	Ee′	h	uvx		8	
2–4	d′	a″Bb′b″	s′s″	Ee′	h	uvx		9	
5	d′d″	a″Bb′b″	s′s″		Hh	uvx		11	
6–7	d′d″	a″Bb′b″	s′s″	Ee′	h	uvx		12	
8	d′d″	Aa′a″	s′s″		Hh	u		13	
9	d″	A a″		Ee′	H	u		14	
10	g[1]				h	u		16	

[1] Dorsolateral seta on abdominal segment 10.

TABLE 12.—*Distribution of setae on* Mimosestes amicus, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area[1]	Epi-pleu-ron	Hypo-pleu-ron	Sternum		Prothorax
Mesothorax		Aa′a″		Ee′			R	6
Metathorax		Aa′a″		e′			R	8
Abdomen								10
1	d′	A		E	h			16
2–5	d′	A a″		e′	h	vx		
6–8	d′	A a″		Ee′	h	x		
9		Aa′a″				vx		
10	g[2]					u		

[1] None present in species.
[2] Dorsolateral seta on abdominal segment 10.

TABLE 13.—*Distribution of setae on* Mimosestes protractus, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area	Epi-pleu-ron	Hypo-pleu-ron	Sternum	Prothorax
Mesothorax	d'd"			e'e"	h'h"	K	2
Metathorax	d'd"			e'e"		K	3
Abdomen							4
1	d'd"	a"	s'		h	uvx	5
2	d'd"	a'a"	s'	e'	h	u x	13
3–5	d'd"	a'a"		e'	h	uv	
6	d'	a'a"		e'	h	uv	
7	d'd"	a'a"		e'	h	u	
8		a'a"		e'			
9	d'					vx	
10	g[1]						

[1] Dorsolateral seta on abdominal segment 10.

TABLE 14.—*Distribution of setae on* Mimosestes sallaei, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area	Epi-pleu-ron	Hypo-pleu-ron	Sternum	Prothorax
Mesothorax		Aa'a"		Ee'		u R	2
Metathorax		Aa'a"		e'		u R	3
Abdomen							4
1	d'	A	s'	E	h	uvx	5
2–4	d'	A a"		e'	h	uvx	7
5–7	d'	A a"		Ee'	h	uvx	9
8	d'	A a"		Ee'	h	vx	12
9		Aa'a"		E	h	v	14
10	g[1]					v	16

[1] Dorsolateral seta on abdominal segment 10.

TABLE 15.—*Distribution of setae on* Neltumius arizonensis, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area[1]	Epi-pleu-ron	Hypo-pleu-ron	Sternum	Prothorax
Mesothorax		Aa'a"		Ee'		R	6
Metathorax		Aa'a"		e'		R	7
Abdomen							8
1	D	a'		E	h	uv	9
2	d'	A		e'	h	uvx	11
3–4	d'	A a"		e'	h	uvx	12
5–6	d'	A a"		Ee'	h	uvx	16
7	d'd"	a"		Ee'	h	uvx	
8	d'	A a"		Ee'	h	uvx	
9		Aa'		E	h	v	
10	g[2]						

[1] None present in species.
[2] Dorsolateral seta on abdominal segment 10.

TABLE 16.—*Distribution of setae on* Sennius morosus, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area	Epi-pleu-ron	Hypo-pleu-ron	Sternum		Prothorax	
Mesothorax		Aa'a"		Ee'		u	R	2	16
Metathorax		Aa'a"		Ee'		uvx	R	3	17
Abdomen								4	
1		A a"	s'	E	h			5	
2–5	d'	A a"		e'	h			6	
6	d'			Ee'	h			7	
7–8	d'	A a"		Ee'	h			8	
9	d'	A a"		E	h			12	
10 g[1]								14	

[1] Dorsolateral seta on abdominal segment 10.

TABLE 17.—*Distribution of setae on* Stator limbatus, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area	Epi-pleu-ron	Hypo-pleu-ron	Sternum		Prothorax	
Mesothorax		a'a"b'		e'e"			K	1	23
Metathorax	d'd"d'''	a'		e'			K	2	
Abdomen								3	
1		a'a"	s'	e'	h	v		4	
2–7		a'a"b'		e'	h	v		5	
8		a'a"b'		e'e"	h	v		6	
9		a'a"		e'	h	v		17	
10 g[1]					h			22	

[1] Dorsolateral seta on abdominal segment 10.

TABLE 18.—*Distribution of setae on* Stator pruininus, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area	Epi-pleu-ron	Hypo-pleu-ron	Sternum		Prothorax
Mesothorax		a'a"b'		e'e"	h		K	2
Metathorax		a'a"b'		e'	h		K	3
Abdomen								4
1	d'	a"	s'	e'	h	uv		5
2–5	d'	a"b'		e'	h	uv		9
6	d'	a"b'		e'e"	h	uv		10
7	d'	a"b'		e'e"	h	uv		12
8		a'a"b'		e'e"	h	v		14
9		a'a"b'			h			24
10 g[1]					h			

[1] Dorsolateral seta on abdominal segment 10.

TABLE 19.—*Distribution of setae on* Stator pygidialis, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area	Epi-pleu-ron	Hypo-pleu-ron	Sternum	Prothorax	
Mesothorax		a'a"b'		e'e"		uv	2	22
Metathorax		a'a"b'		e'		uv	3	
Abdomen							5	
1	d'	a"	s'	e'	h	uv	6	
2–5	d'	a"b'		e'	h	uv	8	
6–7	d'	a"b'		e'e"	h	uv	10	
8		a'a"b'		e'e"	h	v	14	
9		a'a"b'			h	v	15	
10	g[1]				h		17	

[1] Dorsolateral seta on abdominal segment 10.

TABLE 20.—*Distribution of setae on* Zabrotes subfasciatus, *first instar*

Segment	Pro-dor-sum	Post-dor-sum	Spirac-ular area	Epi-pleu-ron	Hypo-pleu-ron	Sternum	Prothorax	
Mesothorax		a'a"		e'	h	K	1	18
Metathorax		a'a"		e'	h	K	2	19
Abdomen							4	20
1	d'd"	a'	,s'	e'e"	h	uv	5	21
2–7	d'	a'a"		e'e"	h	uv	7	22
8		a'a"		e'e"	h	uv	12	23
9		a'a"		e'	h	v	13	24
10	g[1]					u	17	

[1] Dorsolateral seta on abdominal segment 10.